

SYSTEMATICS AND BEHAVIOR
OF SOUTH AMERICAN FLICKERS
(AVES, *COLAPTES*)

LESTER L. SHORT

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ABSTRACT

THE GENUS *Colaptes* is comprised of eight species, formerly arranged in the genera *Colaptes*, *Nesocleus*, and *Chrysoptilus*. More or less distinct forms hybridize in secondary contacts within four of the eight species. The six South American species constitute two subgroups; the forest, or green, flickers, which are more arboreal and more closely resemble the ancestor of *Colaptes*, and the ground flickers, which are to a high degree terrestrially adapted, live in open country, and represent the most specialized species of the genus. The North American *Colaptes auratus* resembles the green flicker group more than it does the ground flickers; it is probably independently derived from an ancestor of the former group. Two well-marked races comprise the somewhat xeric-adapted *C. atricollis*, which is morphologically and behaviorally unspecialized. Several races are included in *C. punctigula*, which is partly ground-foraging and the only truly tropical flicker. *Colaptes melanochloros* forms a super-species with *punctigula*, and it is comprised of two distinctive racial groups, by some authors considered species. The *melanochloros* group of more arboreal, woodland and savanna populations is arranged in two distinct races, *melanochloros* and *nattereri*, which intergrade over a large part of southern Brazil. Three much less strongly marked subspecies, *melanolaimus*, *leucofrenatus*, and *nigroviridis*, constitute the *melanolaimus* group, which inhabits more open country and woodland edges and is partly ground-foraging. The two groups interbreed freely in Corrientes, Argentina, in Rio Grande do Sul, Brazil, and probably in south-central Paraguay, although rather effectively isolated by the Paraguay River in northern Paraguay. *Colaptes pitius*, a monotypic, forest-edge species of Patagonia and Chile, forages on the ground and nests either

arboreally or terrestrially. The northern Andean *C. rupicola* is composed of a southern group of two moderately differentiated races, *rupicola* and *puna*, and a morphologically distinct north Peruvian race, *cinereicapillus*, which also differs somewhat in behavior from the southern forms. Contact between *cinereicapillus* and the more southern forms is limited topographically and ecologically; interbreeding occurs, with some introgression. This highland species is highly social, completely terrestrial, and is the only flicker that does not subsist mainly on ants. There are two rather weakly marked races of the terrestrial *C. campestris*, northern *campestris* with a black throat and southern *campestrisoides* with a white throat. These races have come into secondary contact recently, and they interbreed in the only major area of contact, central Paraguay. Slightly less social than *rupicola*, *campestris* nests in the ground or in fence posts or trees. It is morphologically and behaviorally distinctive, and it appears to be the most specialized of the flickers. The habits, vocalizations, and displays of the various flickers show many similarities. The ground flickers have the most distinct behavioral features, many of which (e.g., walking gait, sociality, yelping calls, wing-flicking display) seem to be adaptations for a terrestrial mode of life. Sympatry within the genus is uncommon and occurs only between distantly related species with divergent plumage patterns and habits. Greater speciation in South America compared with North America probably reflects greater opportunities for speciation on the former continent. *Colaptes* evolved from an arboreal, ant-eating woodpecker that resembled modern species of *Piculus* (e.g., *rivolii*); these genera are very closely related.

INTRODUCTION

THE WOODPECKER GENUS *Colaptes* contains eight species distributed throughout the New World from Alaska to Tierra del Fuego. Among these species, called flickers, are some of the most social woodpeckers. Of these woodpeckers two are especially conspicuous, widespread, and well-known; one is the North American Flicker (*C. auratus*) and the other the Campo Flicker (*C. campestris*) of South America. The genus is important in the Picidae because it contains species that are partly and fully terrestrial, the

antithesis of the arboreal specialization for which this avian family is noted. Within this genus one finds almost a full spectrum of habits from entirely tree-foraging through various part-terrestrial and part-arboreal combinations, to a fully terrestrial existence.

From an evolutionary point of view the genus *Colaptes* is especially interesting, for hybridization occurs regularly in the wild between well-marked forms (indeed these have in each case been treated by some authors as species) in four

of the eight species. These include the hybrid zones and hybrid swarms among the *chrysoides*, *cafer*, and *auratus* groups of *Colaptes auratus* described previously (Short, 1965a), and hybridization in South America between the *melanochloros* and *melanolaimus* groups of *C. melanochloros*, between *C. c. campestris* and *C. c. campestroides*, and between the *rupicola* and *cinereicapillus* groups of *C. rupicola*. The last three situations are discussed in the present report. My previous publications dealing with *Colaptes* mainly treated the North and Middle American species (*C. auratus*, *C. fernandinae*; see Short, 1965a, 1965b, 1967), although certain aspects of the South American flickers also have been reported (Short, 1969b, 1970a). These earlier reports present a framework for consideration of hybridization and of variation, which I generally have followed in the present treatise. I have drawn upon earlier unpublished behavioral studies of *C. auratus* for use in comparisons with South American species in the behavior section below.

The purposes of the present report are several. First, I intend to describe the variation within the South American flickers, especially those involved in situations of hybridization. The three cases of hybridization are analyzed, and effects of interbreeding are evaluated. I present the available information on the habits of these species, and the results of my studies of behavior. These data provide a framework for a discussion of behavior and ecology in relation to the evolution of flickers. Finally, I offer a hypothesized phylogeny of the entire genus, based on all aspects of morphological and behavioral information at my disposal.

METHODS AND MATERIALS

Comparative studies of specimens involved use of standard museum procedures. I obtained measurements of wing length (chord), tail length, bill length (from nostril, unless otherwise stated), tarsal length, and other measurements described below. Statistical treatment was utilized where warranted, usually for samples containing five specimens or more.

In the course of my studies over the past 15 years I have examined more than 5,000 specimens of the various species discussed herein. With the help of field assistants I collected 111 specimens of South American flickers (*Colaptes campestris*, 10; *C. rupicola*, 28; *C. pitius*, 12; *C.*

melanochloros, 58; *C. punctigula*, 2; and *C. atricollis*, 1). These specimens are in the collection of the American Museum of Natural History, except for a few in the Museo Argentino de Ciencias Naturales in Buenos Aires. Specimens were examined from the collections of the following institutions:

AMNH, the American Museum of Natural History
 ANSP, Academy of Natural Sciences of Philadelphia
 BM, British Museum (Natural History), London
 CM, Carnegie Museum, Pittsburgh
 CU, Cornell University collections, Ithaca
 FMNH, Field Museum of Natural History, Chicago
 IML, Instituto "Miguel Lillo," Tucumán, Argentina
 LAM, Los Angeles County Museum
 MACN, Museo Argentino de Ciencias Naturales, Buenos Aires
 MAK, Museum Alexander Koenig, Bonn, Germany
 MCZ, Museum of Comparative Zoology, Harvard University, Cambridge
 MHNP, Musée d'Histoire Naturelle, Paris
 MLP, Museo de La Plata, La Plata, Argentina
 MN, Museu Nacional, Rio de Janeiro, Brazil
 MNHL, Museum of Natural History, Leiden, Netherlands
 MNHN, Museo Nacional de Historia Natural, Montevideo
 MVZ, Museum of Vertebrate Zoology, University of California, Berkeley
 NHMW, Naturhistorisches Museum, Vienna
 NMM, Naturhistorisches Museum, Munich
 PMNH, Peabody Museum of Natural History, Yale University, New Haven
 PMZ, Princeton Museum of Zoology, Princeton University, Princeton
 SM, Senckenberg Museum, Frankfurt
 SMNH, Swedish Museum of Natural History, Stockholm
 UCLA, University of California, Los Angeles collection
 UKMNH, University of Kansas Museum of Natural History, Lawrence
 UMMZ, University of Michigan Museum of Zoology, Ann Arbor
 USNM, United States National Museum, Smithsonian Institution

Observations in the field were aided by the use of 8 by 40 field glasses. Moving pictures and tape recordings supplemented field observations. We used a Bolex 16 mm. camera with various lenses for moving pictures. Tape recordings were obtained with a Uher 4000-L Report Tape Recorder with Uher MD 514 Dynamic microphone mounted in a 24-inch parabolic reflector and operated at 7.5 inches per second. Repre-

sentative vocalizations were analyzed by sound spectrograph having both narrow and wide band filters.

ACKNOWLEDGMENTS

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appreciated. I am grateful to all of these persons, and to many others who aided me in one way or another.

I wish to thank the various curators who lent me specimens necessary for the study (see list above), and particularly those who assisted me while I studied in the collections in their charge. The latter include: Dr. E. R. Blake and Mr. M. Traylor at the Chicago Field Museum of Natural History; Drs. R. Zusi, R. Banks, and A. Wetmore, and Mrs. R. Laybourne at the U. S. National Museum; Drs. Parkes and M. Clench at the Carnegie Museum; Dr. K. Stager at the Los Angeles County Museum; Dr. N. K. Johnson at the Museum of Vertebrate Zoology, Berkeley; Drs. Robert W. Storer and R. Payne at the Museum of Zoology, University of Michigan; Dr. R. Mengel at the University of Kansas Museum of Natural History; Dr. R. Paynter, Jr. at the Museum of Comparative Zoology, Harvard University; Dr. Olrog at the Miguel Lillo Institute, Tucumán, Argentina; Dr. Navas at the Museo Argentino de Ciencias Naturales in Buenos Aires; Drs. G. Rokitansky and H. Schifter at the Natural History Museum, Vienna, Austria; Drs. G. Niethammer, F. Sauer, and H. E. Wolters at the Museum Alexander Koenig, Bonn, Germany; Dr. G. Diesselhorst at the Natural History Museum, Munich, Germany; Dr. J. Steinbacher at the Senckenberg Museum, Frankfurt, Germany; Mr. D. Goodwin at the British Museum (Natural History); Dr. J. Dorst at the Natural History Museum, Paris; and Dr. G. F. Mees at the Natural History Museum, Leiden, Netherlands.

SYSTEMATICS AND HYBRIDIZATION

GENUS COLAPTES

I HAVE PROVIDED below a résumé of the genus *Colaptes* as a prelude to a discussion of the systematics of the included species. The eight species I recognize have been placed in as many as five genera. Currently (e.g., Meyer de Schauensee, 1966, 1970) three genera usually are recognized, namely *Colaptes*, *Nesocoeleus*, and

Chrysoptilus, although the authority on West Indian birds, J. Bond (1966) recently has accepted my (1965b) merger of *Nesocoeleus* into *Colaptes*. All scientific names mentioned herein are included in Peters (1948), who cited the pertinent publications.

COLAPTES VIGORS, 1825

INCLUDED "GENERA": *Chrysoptilus* Swainson, 1831, *Soroplex* Gloger, 1842, *Pituipicus* Bonaparte, 1854, *Nesocoeleus* Sclater and Salvin, 1873.

DIAGNOSIS: Resembling *Piculus* Spix, 1824, but entirely barred above and part-terrestrial to terrestrial in habits. Other features are: bill very narrow across culmen especially between nostrils; culmen curved generally throughout its length; bill tip pointed, little chisel-shaped; skull bones thin, not massive and heavy; skull projections for muscle attachment weakly developed compared with arboreal genera, including *Piculus* and *Picus*; underwings yellow or reddish, especially feather shafts; tail with some yellow or red in shafts and some or much of the same color on the feather vanes; tail partly or fully barred; sexes differ in malar color, but sexual differences reduced in several terrestrial species; plumage usually with large markings (or even a patch) concentrated on breast, in some cases including throat; diet mainly ants; vocally active, noisy woodpeckers.

TYPE SPECIES: *Colaptes auratus* (Linnaeus, 1758).

INCLUDED SPECIES: *atricollis*, *punctigula*, *melanochloros*, *auratus*, *rupicola*, *piti*us, *campestris*, *fernandinae*.

REMARKS: The genera *Colaptes* and *Piculus* are so closely allied that the distinction between them is not great. Until further morphological and behavioral studies, which might show greater (or less) distinction of these genera, are made, they are not merged. They can best be defined by their habits. Species of *Colaptes* are conspicuous, vocal woodpeckers that feed on ants and forage occasionally to entirely on the ground. Species of *Piculus* are less conspicuous, not very vocal, and do not forage on the ground. The barred back of the species of *Colaptes* serves to distinguish that genus morphologically from

Piculus. Species of *Piculus* also are largely distinguished from *Colaptes* by their more massive, specialized ("woodpecking") skull with greater prominence of its bony projections such as the orbital shelf, and the broader base (across culmen between nostrils) of bill. Among species of *Piculus* the *Piculus* subgroup, including "*Hypoxanthus*," seems closest to the flickers. The little known *Piculus rivolii* (Short, 1970a) and *P. rubiginosus* are like the smaller green flickers (*C. punctigula*, *C. atricollis*) in habits and morphology, but are strictly arboreal, quiet woodpeckers which do not forage terrestrially.

Elsewhere I have discussed (Short, 1965b) my reasons for merging monotypic *Nesocoeleus* (*fernandinae*) into *Colaptes*. The genus *Nesocoeleus* is based essentially on a single character, bare (unfeathered) nostrils. Although we do not understand the biological significance of this feature, I have noted (1965b) that other genera show variation in the amount of feathering about the nostrils. To those examples mentioned (1965b) I add the cases of *Celeus*, species of which vary in the amount of feathering that abuts on (but does not cover) the nostrils, and *Dryocopus*, most species of which have feathered nostrils, but *D. galeatus* has unfeathered nostrils. I do not believe that this feature should be used as a diagnostic generic character, especially for definition of a monotypic genus. Nevertheless, this feature and its odd combination of color patterns make *Colaptes fernandinae* the most distinct species within the genus, perhaps meriting subgeneric separation apart from the other species.

The genera *Soroplex* (*campestris*, *rupicola*) and *Pituipicus* (*piti*us) have long been merged in *Colaptes* by most taxonomists. These include the most terrestrially specialized flickers. Taken as a single group, they differ somewhat from the

other species of the genus *Colaptes* in having: strongly developed tubercles on the ulna; a strongly pronged manubrial spine on the sternum; a relatively broader, flatter bill; and more social habits. The species are distinct within the group, and each species has special features not found elsewhere in the genus. Among these features are the very long bill and wide premaxillae of *rupicola*, the all-barred plumage of *pitius*, and the gold breast patch and very broad bill of *campestris*. Additionally, *rupicola* and *campestris* frequently walk on the ground, a trait unknown in other flickers. Nevertheless, the habits and vocalizations of these species and many features of their morphology indicate their congeneric relationship with other flickers.

The genus *Chrysomitris* had not been merged in *Colaptes* prior to my determination (1965a) that it is congeneric with the other flickers. The green, or forest flickers are the least terrestrially adapted, and probably most closely resemble the ancestor of *Colaptes*. Indeed, it is likely that the *melanochloros-punctigula* group is more closely related to *C. auratus* than is the latter to the "*Soroplex*" species. I note for example that replacement of brown by green in the plumage of *C. auratus*, as occurs to some degree in variant specimens of Cuban *C. a. chrysocaulosus*, gives a very "*Chrysomitris*"-like plumage. The vocalizations and displays of *atricollis*, *punctigula*, and *melanochloros* closely resemble those of *C. auratus*, and like the latter the former species are not highly social as are species of "*Soroplex*." The tubercles on the ulna are generally much weaker than in *Soroplex* and about like those of the *chrysocaulosus* group of *Colaptes auratus*. The green flickers resemble *Colaptes auratus* in their bill structure, and in having a weakly pronged manubrial spine. I find no trenchant characters on which to base generic separation of these green flickers from *Colaptes*.

The ranges of the species of *Colaptes* are shown in figure 1.

COLAPTES ATRICOLLIS (MALHERBE)

The Black-necked Flicker is endemic to Peru (fig. 1), occurring in two disjunct populations, one along the northwest coast and western slopes of the Andes, and the other in and adjacent to the arid Marañon Valley of north-central Peru. Both are found in scrub desert vegetation (but see below), although they seem to have accommodated to man's cultivation, as

they frequent orchards and shade trees to some degree. The tolerance of this flicker for desert conditions is matched in *Colaptes* only by some western Argentine and Bolivian highland populations of the *melanolaimus* group of *C. melanochloros*, and by the desert North American *chrysoides* group of *C. auratus*. This species is slightly larger than *punctigula*; it overlaps somewhat with smaller specimens of *C. melanochloros nattereri* and with *C. auratus gundlachi*.

Major features of *atricollis* are its fully and narrowly barred underparts (as *C. fernandinae*, and *Piculus* sp.), a completely barred rump (only *fernandinae* otherwise has this among *Colaptes*), and a fully black throat grading into the breast barring (not truncate at rear of throat as *C. campestris campestris*, the only other "black-throated" flicker). This flicker also shows sexual dimorphism in two color patterns: (1) red color extends from nape forward at sides of crown to lores or forehead of male, only to nape of female; and (2) male with a red malar stripe, female with a black. Only *punctigula* among other flickers has red color extending forward lateral to the crown, but this occurs in some males and not others of that species. In no other flicker is the malar stripe of the female fully black. The crown of *atricollis* is gray rather than black (as in *punctigula* and *melanochloros*), although black traces are evident. In this feature it tends toward *C. rupicola*, and also to some extent toward *C. auratus* (in part) and *C. pitius*.

The back bars of *atricollis* vary from narrow bars on a solidly colored (green) background, as in *punctigula*, *auratus* (except *mexicanoides*), and some individuals of *melanochloros* (*melanochloros* group), to broader bars on a mixed pale and darker background giving a tricolored appearance as in the *melanolaimus* group of *C. melanochloros* and the *mexicanoides* group of *C. auratus*. The rectrices show much yellow dorsally, as in *C. punctigula* and approaching *C. fernandinae*, but not other flickers. The feather shafts of the remiges are yellow dorsally in one subspecies, as in *C. auratus*, *C. punctigula*, and the *melanolaimus* group of *C. melanochloros*; in the other subspecies they are dusky above as in *C. m. melanochloros*. The inner remiges are more strongly barred than in other flickers, except *fernandinae*. The tail is rather strongly barred as in *punctigula* and the upper tail coverts are regularly and fully barred as in some species of *Piculus* and many flickers.

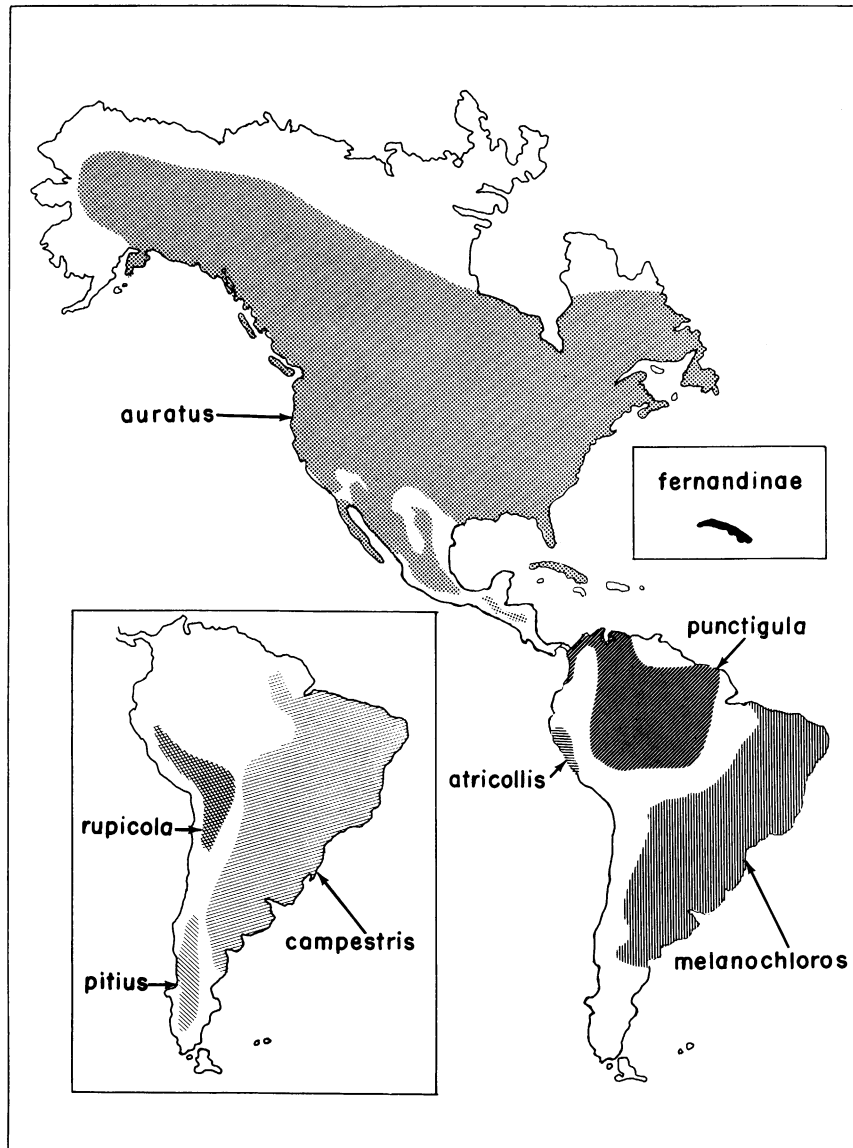


FIG. 1. Distribution of species of *Colaptes*. Note that sympatry occurs only between *C. auratus* and *fernandinae*, and between *C. campestris* and *melanochloros*. *C. rupicola* and *melanochloros* may meet in Bolivia and Argentina, and *C. punctigula* may contact *melanochloros* in Mato Grosso.

Colaptes atricollis bridges a gap in wing length between *C. punctigula* and *C. melanochloros nattereri* (113 to 125 mm.). It has a very long tail, the tail/wing ratio equaling or exceeding that of *C. m. melanochloros* (ratio 0.72 to 0.84), thus differing from *punctigula*. The relatively long bill (21 to 26 mm.) is longer than that of many, larger individuals of the *melanochloros* group of

C. melanochloros. The tarsus is moderately long (22 to 25 mm.).

I was unable to investigate fully the molts and variation in the juvenal plumage of Black-necked flickers. Young birds seem essentially like adults, although varying somewhat more in ventral barring. Individual variation in barring, both above and below, is considerable. There is

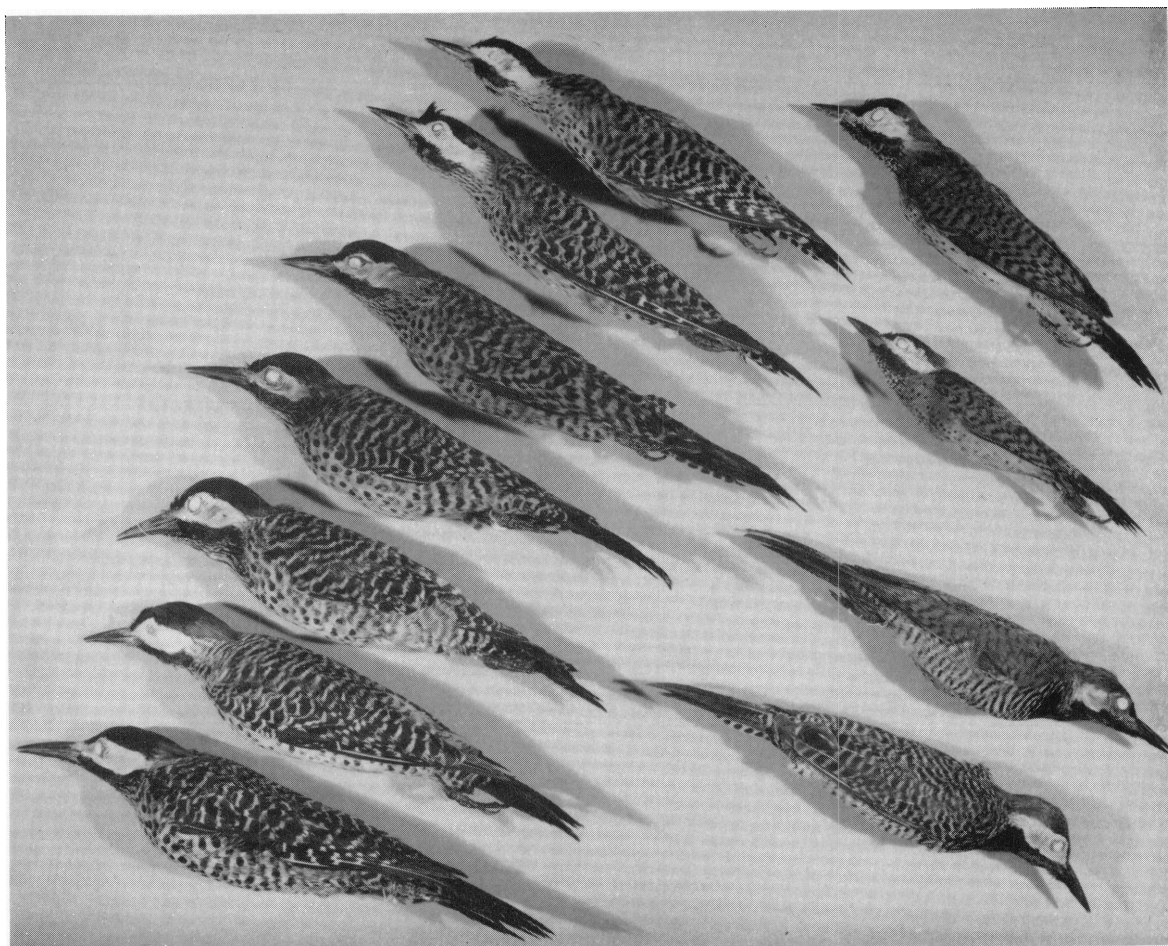


FIG. 2. The green, or forest flickers. Clockwise from bottom left are males of: *Colaptes melanochloros leucofrenatus* ("patagonicus," S Buenos Aires), *C. melanochloros melanolaimus* (Bolivia), *C. m. leucofrenatus* (Entre Ríos), *C. m. melanochloros* × *nigroviridis* (Ituzaingó, Corrientes), *C. m. melanochloros* (Misiones), *C. m. melanochloros* > *nattereri* (= "cristatus," NE Paraguay), *C. m. nattereri* (Mato Grosso), *C. punctigula guttatus*, *C. p. punctigula*, all facing left, and *C. atricollis atricollis* and *C. a. peruvianus*, facing right. Note especially variation in size, darkness of light bars, bill and tail length of *C. melanochloros*, in size of *C. punctigula*, in back barring of *C. atricollis*, and note shift from throat to breast markings in *C. melanochloros* versus *C. punctigula* (see text).

variation among males in the penetration of the gray-black crown by red. Some birds have spots instead of bars present on the flanks.

Geographic variation is straightforward, to some extent paralleling that of *C. melanochloros*. The coastal and interior populations have differentiated rather strongly because they are essentially isolated geographically by the Andes Mountains. The coastal and western mountain slope form, *C. a. atricollis*, differs from the interior *C. a. peruvianus* as follows (see fig. 2): dorsally narrowly barred on green background, versus

tricolored, with wider dark bars on a mixed greenish and buff background in *peruvianus*; underparts generally fully barred, compared with *peruvianus*, which has an unbarred, pale belly; rump fully barred in both races, but background green like the back in *atricollis*, whereas the back is paler, even white occasionally in *peruvianus*; remiges have shafts with dark pigment, whereas *peruvianus* has little or no dark pigment; and tail/wing ratios average greater in *atricollis*. The only weight information available to me is the weight of an adult male from the Santa

Eulalia Valley east of Lima, Peru, taken on August 29 (89.8 gm.; *C. a. atricollis*).

It seems likely that *atricollis* evolved originally as a forest or woodland west coastal Peruvian derivative of an ancestor in common with the ancestor of *punctigula* and *melanochloros*. Adaptation to more arid scrub woodland came later and perhaps not fully, for characters of the two extant subspecies suggest that the western populations (ancestral *C. a. atricollis*) essentially remained woodland inhabitants (riparian woods, and forest originally on western Andean slopes, as exist today at Zarate, above Lima), whereas the interior populations (ancestral *peruvianus*) did become desert-adapted. The subspecies of *atricollis* are:

Colaptes atricollis atricollis (Malherbe, 1850)

Colaptes atricollis peruvianus Reichenbach, 1854

Colaptes atricollis lymani Bangs and Noble is considered a synonym of *peruvianus*

COLAPTES PUNCTIGULA (BODDAERT)

The widespread tropical Spot-breasted Flicker is the only South American flicker reaching Middle America (fig. 1). It is the smallest of the flickers, although larger races attain the size of some specimens of *Colaptes atricollis* and *Colaptes melanochloros* (*nattereri*). Generally, this species resembles *Colaptes melanochloros* quite closely, and its range complements the range of the latter. There are no known areas of contact between *punctigula* and *C. m. nattereri*, the adjacent race of *melanochloros*, but the two approach each other closely in Bolivia (*nattereri* in northern Santa Cruz, *punctigula* in Beni) and perhaps in northern Mato Grosso. There appears to be a hiatus in their distribution in eastern Pará, although *nattereri* occurs on Marajo Island, and *punctigula* may reach the Atlantic Coast on the adjacent mainland north of the Amazon.

In addition to its smaller size, *punctigula* differs from *melanochloros* in its generally scalloped black throat streaks, caused by the white of the throat tending to form spots (the only *Colaptes* thus resembling *Piculus*, e.g., *P. rubiginosus* which varies in this feature exactly as *punctigula*). The streaks of *melanochloros* are equal throughout, or broader at the rear, never narrowest in their center. Several races (see below) of *punctigula* have reduced black in the throat, forming narrow streaks like *melanochloros*, although indications of "scalloping" effects are still noticeable. There is a

sharp demarcation between the ventral spotting and throat streaking in *punctigula*, whereas the throat streaks (see fig. 2) grade completely into the ventral spots of *melanochloros*. Another major trait in *punctigula* is the strong tendency for red to occur on the breast (especially males). In some cases the red nape patch extends anteriorly along the crown of males, as is typical of *C. atricollis*, but not *melanochloros*. *Colaptes punctigula*, like *atricollis*, has extensive yellow dorsal feather shafts of the rectrices, which are mainly black in *melanochloros*. Other tendencies away from *melanochloros* are: the generally narrower dorsal bars; the finer, often rounder and deeper (rather than wide) ventral spots; and the concentration of dark olive on the breast. Mensural overlap with other flickers involves wing length (barely, with *atricollis*), bill length (with both *atricollis* and *C. melanochloros nattereri*), and tarsal length (with *atricollis*). Tail/wing ratios range from 0.56 to 0.66, below that of *C. atricollis* and of *C. m. melanochloros*, but within the range of other races of *C. melanochloros*. Weights available for *punctigula* indicate a range of from 50 to 70 gm. for *C. p. punctigula*, and of at least 75 to 79 gm. for *C. p. speciosus*, about 10 to 20 gm. less than *C. atricollis*, and only half the weight of *C. m. melanochloros* and *C. m. nigroviridis*.

The remiges of *punctigula* usually lack dark pigment in the shafts, or they have only traces, as in *C. atricollis peruvianus* and the *melanolaimus* group of *C. melanochloros*. The upper tail coverts are fully and evenly barred. The tail generally is barred on rectrices 1, 4, 5, and 6 as in *C. atricollis* and *C. melanochloros*.

Individual variation in addition to that indicated so far in this discussion involves the overall brightness (olive versus yellow-green) of the plumage, the depth of the barring dorsally, the number, size, and shape of the ventral spots, and the extent of red on the rear of the crown. Juvenal birds are more diverse than adults. Some young flickers have reduced spotting, even in well-spotted races, but most juveniles tend to be more heavily spotted than adults. The spots may be barlike, or they may converge on the anterior breast causing a black area to be formed. Studies of the juvenal plumage and molts of the only wet Tropical Zone species of *Colaptes* would be rewarding, but such studies have not yet been made.

I have not attempted a thorough investigation of the subspecies of this flicker, but I shall

summarize the results of a brief study of specimens, mainly those in the American Museum of Natural History. Geographic variation is not marked, with the exception of the arid northern Colombian *C. p. ujhelyii*. This subspecies has its dorsal barring very reduced; most specimens have only fine, pale bars not reaching the borders of the feathers, but a few have the bars obsolete. The rump is much brighter than is the back in this race, and ventral spots are sparse and fine. This form closely resembles *melanochloros* in throat color, with narrow black malar streaks almost lacking indications of the "scalloping" or narrowing of the centers of the black streaks. Among other races of *punctigula*, variation involves (see fig. 2): size from small as in *C. p. punctigula* to large as in *C. p. speciosus*; general dorsal color from bright yellow-green to dull green (*punctipectus*) and olive (some *speciosus*); throat and (females only) malar streaks from narrow in *striatigularis* (as in *ujhelyii*) to mainly black with white spots, as in most races (especially *zuliae*, *speciosus*, and *guttatus*); ventral color, ranging from bright yellow posteriorly and greenish anteriorly to almost concolored (some Amazonian birds); size and number of ventral spots, varying from generally fewer, finer spots (*punctipectus*, *punctigula*, as well as *ujhelyii*), to many large spots (*speciosus*, *guttatus*, even becoming bar spots as some *melanochloros*); breast color, from dark green (*guttatus*, *speciosus*) to paler green; and amount of red on breast.

The following are the subspecies of *punctigula*:

- Colaptes punctigula punctigula* (Boddaert, 1783)
- Colaptes punctigula rubidipectus* Todd, 1946
- Colaptes punctigula guttatus* (Spix, 1824)
- Colaptes punctigula speciosus* (Malherbe, 1862)
- Colaptes punctigula zuliae* Cory, 1915
- Colaptes punctigula punctipectus* Cabanis and Heine, 1863
- Colaptes punctigula striatigularis* Chapman, 1914
- Colaptes punctigula ujhelyii* Madarász, 1912

I consider *C. p. lutescens* Griscom a synonym of *striatigularis*, and *C. p. notatus* Cory a synonym of *punctipectus*. The latter, known from a single specimen from "Colombia," may be an aberrant immature *punctipectus*. Otherwise, the subspecies listed are those presented in Peters (1948).

COLAPTES MELANOCHLOROS (GMELIN)

INTRODUCTION

The situation existing between the *melanochloros* and *melanolaimus* groups of *Colaptes melanochlo-*

ros has attracted the interest of various workers. The present report is the fourth treating the entire complex. The previous studies are those of Cory (1919), Laubmann (1934), and Traylor (1951). Other investigators have treated portions of the complex taxonomically (see citations in Traylor, 1951). My own studies essentially corroborate the taxonomic conclusion of Laubmann that the various forms in this group are conspecific, although some races recognized by him are not recognized herein. Traylor treated 10 subspecies, five each in the species *C. melanochloros* and *C. melanolaimus*, based upon studies of 245 specimens. The analysis herein is the result of studies of 775 adult specimens and about 80 immature flickers. These include many recently taken specimens that were unavailable to earlier workers and especially material, some obtained by myself and my associates, from critical areas in Argentina (Corrientes) and Brazil (Rio Grande do Sul).

The western and southern *melanolaimus* group varies relatively little in color, but varies somewhat in measurements. The group occupies edges of woodlands and dry woodlands of the Chaco, the pampas, and dry subtropical woodland in the lowlands, and arid scrub and riparian vegetation in the mountains of western Argentina and Bolivia. Individuals of at least several races of this group feed part of the time on the ground near trees. The *melanochloros* group occupies subtropical moist forest, riverine forest, savannas, scrub woodland, and woodland edges in Brazil, eastern Bolivia, and eastern Paraguay. Two rather distinct subgroups of this group are the larger, longer-tailed, and greener forest populations of the southeast, and the smaller, shorter-tailed, and paler scrub woodland and savanna populations of the north and west. No flickers of these last two subgroups have been seen on the ground, although the savanna form may forage on the ground. Geographical variation in these groups and subgroups, and their interactions in areas where they approach and meet one another form the major portion of the discussion below.

Individual variation is rather great in this species. The sexes differ in color of the malar stripe, which is black overlain with red in males, and black more or less (geographically variable) flecked with white in females. There are slight differences in measurements, females having shorter wings, proportionally and even actually

longer tails, shorter bills, shorter tarsi, and greater tail/wing ratios. Other tendencies are noted below.

Juvenal flickers generally have larger, more streaklike spots below, broader black streaking on the throat and malar, tending to extend onto the breast (thus, the demarcation of throat streaks and breast spots in adults is lacking), greener underparts (*melanolaimus* group), more barred posterior underparts, more varied upperparts (greener in *melanolaimus* group, more variegated in *melanochloros* group), a less conspicuous rump patch (in groups having the patch), and a longer and broader outer primary feather than adults. They also can be distinguished by their fluffier plumage (especially on the abdomen, a character useful in determining the age of most woodpeckers). Juvenal flickers of the two groups are more alike in plumage than are adults.

Abnormal variation in coloration is not great. Occasional birds show some red in the black on the crown, particularly laterally. This may reflect an ancestral condition of an all-red crown found in relatives of the genus *Piculus*. Red occasionally may occur also in the golden throat-breast patch of the *melanolaimus* group (especially southern *leucofrenatus* specimens), and in the rump or even the back of flickers of the *melanochloros* group.

Seasonal variation is considerable, affecting various mensural traits and overall coloration. Fresh-plumaged birds have of course longer wings and tails than worn birds (1 to 3 per cent seasonal variation). Seasonal differences in bill length are slight, and more and larger samples are needed to detect seasonal variation. Generally birds are greener, brighter, and lighter colored in fresh plumage. This reflects fading of the green and wear of the pale edges of dorsal and ventral feathers, which render the more basal, dark barred or spotted portions more visible. Worn birds from western Argentina or Bolivia are deep black, with pale edging reduced to fine lines, or even absent. Allowance was made for these factors in studying geographical variation; similarly plumaged birds were compared whenever possible, and excessively worn birds were discarded from consideration.

Molt will not be described in detail herein. The annual molt occurs following the breeding season, as in most birds. This usually takes place within the period of February to June, varying

from region to region. Molting birds of course were not measured (wing, tail) when measurements would be affected by the molt. Such birds were treated with care because of the mixed appearance of different color patterns, especially the upperparts, underparts and throat-breast patch. The juvenal plumage acquired after hatching is molted within one to three months after the young leave the nest. The molt appears to be complete in contrast to *Colaptes auratus* in which young birds frequently retain their secondaries until their first annual molt (the year after hatching). As in *C. auratus* (*auratus* group) the shafts of the remiges are paler yellow in juveniles than in adults, and this is especially true of the secondaries (which fade less than the more exposed primaries).

The possibility of some migration in the southernmost populations is discussed below (see *C. m. leucofrenatus*).

BACK COLOR (TABLE 1): Back color was rather subjectively tabulated, using various categories and evaluating them seasonally. The green-backed condition of *C. m. melanochloros*, in which back feathers are barred with brown-black and green is one category. The opposite extreme is the variegated, almost quadricolored (brown-black bars with brownish, gold, and whitish interspaces) condition of fresh-plumaged specimens of *C. m. leucofrenatus*. However, *leucofrenatus* in worn plumage may appear simply brown-black and white or dusky white. Gradient intermediate categories of green with some paler color, mixed green and gold-brown, and brown-gold-white with green traces were recognized. The sexes differ little or not at all in this feature.

RUMP COLOR: Two parameters of rump coloration were evaluated in distinguishing a rump patch from lack of a patch. The background color ranges from green or yellow-green, concolored with the back in *C. m. melanochloros*, through bright green-yellow and yellow (*nattereri*) to white (*leucofrenatus*). Some birds have gold or even red in the rump feathers. A subsidiary feature is variation in the rump markings with a range from fully spotted or barred to spotless. The last condition occurs uncommonly in the yellowish-rumped *nattereri* (and to a certain extent in *Colaptes punctigula*, occupying a range adjacent to *nattereri*), and in the *melanolaimus* group. Generally, however, the rump bears strong markings, and it is the background color that is emphasized. Numerical scores were

TABLE 1
ANALYSIS OF BACK COLOR AND EAR COVERT COLOR IN *Colaptes melanochloros*^a

Sample	Back Color						Ear Covert Color					
	N	ml	>	i	<	mc	N	ml	>	i	<	mc
<i>melanochloros</i> Group												
<i>nattereri</i> E ^b	16	0	0	4	1	11	16	8	0	5	2	1
<i>nattereri</i> W ^c	85	0	0	12	10	63	83	38	3	17	1	24
E São Paulo	4	0	0	1	1	2	4	2	0	0	1	1
Espírito Santo ^d	8	0	0	0	0	8	8	0	0	1	1	6
NW São Paulo	9	0	0	1	0	8	9	1	0	4	0	4
SE Paraguay	16	0	0	0	0	16	16	0	0	0	2	14
<i>melanochloros</i> ^e	115	0	0	0	11	104	113	0	0	2	12	99
NE R. G. do Sul	16	0	0	4	2	10	16	5	0	1	2	8
Corrientes Transects												
Ituzaingó	12	0	0	3	5	4	13	0	1	3	3	5
Ituzaingó W	3	1	1	1	0	0	3	1	1	1	0	0
Itá-Ibaté	15	5	2	7	1	0	15	8	3	1	3	0
San Carlos	6	0	0	3	2	1	6	2	1	1	1	1
Est. del Iberá	8	5	2	1	0	0	7	7	0	0	0	0
SW Corrientes	12	12	0	0	0	0	12	12	0	0	0	0
Colonia Garabí	6	0	0	0	1	5	6	1	0	0	0	5
Cuay Grande	6	0	1	1	1	3	6	1	0	0	3	2
Torrent	31	0	0	4	17	10	17	3	0	7	0	7
Alvear	5	0	0	2	1	2	5	4	0	0	0	1
<i>melanolaimus</i> Group												
Uruguay	13	5	0	8	0	0	14	12	0	0	0	2
Entre Ríos	47	38	0	9	0	0	46	40	1	3	0	2
<i>nigroviridis</i> SE ^f	39	19	4	9	7	0	41	30	4	7	0	0
<i>nigroviridis</i> NW ^g	45	8	4	18	11	4	45	35	2	8	0	0
NW Entre Ríos ^h	13	12	1	0	0	0	14	12	1	1	0	0
W Formosa	4	4	0	0	0	0	4	4	0	0	0	0
Santiago d. Estero	12	12	0	0	0	0	7	7	0	0	0	0
<i>leucofrenatus</i> ⁱ	94	72	6	11	5	0	94	92	1	1	0	0
Salta	19	15	2	1	1	0	20	17	0	3	0	0
<i>melanolaimus</i>	40	28	1	2	6	3	40	30	8	2	0	0

^a All adults are included. ^b Ceará, Piauí, Pernambuco, SE Bahia. ^c Bolivia, Mato Grosso, NW Bahia, Goiás, NW Minas Gerais, Maranhão, Pará, NE Paraguay. ^d Includes Rio de Janeiro. ^e Misiones, S São Paulo, S Paraná, Santa Catarina. ^f SE Formosa, E Chaco, NW Corrientes, NE Santa Fe. ^g W Paraguay, N Formosa, Villa Montes area of Bolivia. ^h Includes eastern border of Santa Fe. ⁱ W Santa Fe, Córdoba, Tucumán, Mendoza, San Luis, Buenos Aires, Río Negro, La Pampa.

Symbols: N, sample size; ml, as *melanolaimus* group; >, tending toward *melanochloros*; i, intermediate; <, tending toward *melanolaimus*; mc, as in *melanochloros* group. In worn birds only ml, i, and mc may be determinable.

not assigned because of the nature of the variation, and especially because the bright yellow or yellow-gold, relatively little-spotted rump of *nattereri* cannot be scored with regard to *C. m. melanochloros* and the *melanolaimus* group, for it is not really intermediate between them. There is no sexual difference in this trait.

REMIGIAL SHAFT COLOR (TABLE 2): The dark pigment in the shafts of *melanochloros* diminishes toward *nattereri* and especially toward the *melanolaimus* group. A graded series of conditions

was established, namely: dark, extensive pigmentation (rendered ++), dark, moderately extensive pigmentation (+), traces of dark pigment (tr), and dark pigment absent (0). There is a slight but consistent sexual difference; females tend to be more heavily pigmented, scoring ++ more often in *C. m. melanochloros*, and showing traces of pigment in more cases than males in the *melanolaimus* group.

EAR COVERT COLOR (TABLE 1): This is another unidirectionally varying character, with

TABLE 2
ANALYSIS OF REMIGIAL BASE COLOR AND AMOUNT OF BLACK AT REAR
OF MALAR AREA IN *Colaptes melanochloros*^a

Sample	Remigial Bases					Rear of Malar Area									
	N	O	tr	+	++	Males N	++	+	+-	=	Females N	++	+	+-	=
<i>melanochloros</i> Group															
<i>nattereri</i> E ^b	16	10	5	0	1	9	0	3	0	6	7	1	2	1	3
<i>nattereri</i> W ^c	62	28	21	12	1	58	0	14	7	37	34	0	8	3	23
E São Paulo	4	2	0	1	1	3	0	2	0	1	1	0	0	0	1
Espírito Santo ^d	8	1	1	3	3	4	0	1	0	3	4	0	0	1	3
NW São Paulo	9	2	3	3	1	6	0	1	1	4	3	0	2	1	0
SE Paraguay	16	0	0	8	8	16	0	6	4	6	6	0	3	1	2
<i>melanochloros</i> ^e	114	0	2	49	63	56	0	8	4	44	43	5	10	4	25
NE R. G. do Sul	16	1	3	8	4	10	0	2	1	7	8	0	3	1	4
Corrientes Transects															
Ituzaingó	12	2	4	6	0	8	1	4	2	1	4	1	1	1	1
Ituzaingó W	3	0	2	1	0	1	0	1	0	0	2	2	0	0	0
Itá-Ibaté	15	6	6	3	0	8	0	4	1	3	7	1	5	0	1
San Carlos	6	4	1	1	0	4	0	1	1	2	2	0	1	1	0
Est. del Iberá	8	4	3	1	0	5	3	2	0	0	3	3	0	0	0
SW Corrientes	12	10	2	0	0	4	2	2	0	0	8	7	1	0	0
Colonia Garabí	6	0	1	5	0	4	1	0	1	2	2	0	0	1	1
Cuay Grande	6	2	3	1	0	3	0	1	1	1	3	0	0	0	3
Torrent	31	8	13	10	0	14	0	6	2	6	17	0	6	2	9
Alvear	5	2	1	2	0	1	0	1	0	0	4	1	2	0	1
<i>melanolaimus</i> Group															
Uruguay	14	11	2	1	0	6	2	3	1	0	7	5	0	1	1
Entre Ríos	47	44	3	0	0	18	16	2	0	0	29	23	5	0	1
<i>nigroviridis</i> SE ^f	40	30	10	0	0	20	10	9	0	1	20	9	9	0	2
<i>nigroviridis</i> NW ^g	45	39	6	0	0	26	9	12	3	2	19	2	13	2	2
NW Entre Ríos ^h	14	13	1	0	0	6	5	1	0	0	8	8	0	0	0
W Formosa	4	4	0	0	0	2	2	0	0	0	2	1	1	0	0
Santiago d. Estero	12	11	1	0	0	6	6	0	0	0	6	3	3	0	0
<i>leucofrenatus</i> ⁱ	96	87	9	0	0	42	42	0	0	0	55	53	1	1	0
Salta	20	18	2	0	0	8	7	1	0	0	12	11	1	0	0
<i>melanolaimus</i>	40	35	5	0	0	23	23	0	0	0	21	21	0	0	0

^a All adults included for remigial bases. ^b Ceará, Piauí, Pernambuco, SE Bahia. ^c Bolivia, Mato Grosso, NW Bahia, Goiás, Maranhão, Pará, NW Minas Gerais, NE Paraguay (last for rear of malar only). ^d Includes Rio de Janeiro. ^e Misiones, S São Paulo, S Paraná, Santa Catarina. ^f SE Formosa, E Chaco, NW Corrientes, NE Santa Fe. ^g W Paraguay, N Formosa, Villa Montes area of Bolivia. ^h Includes eastern border of Santa Fe. ⁱ W Santa Fe, Córdoba, Tucumán, Mendoza, San Luis, Buenos Aires, Río Negro, La Pampa.

Symbols for remigial bases are: N, sample size; 0, dark pigment absent; tr, traces of dark color; +, moderate dark color; ++, extensive dark color. Symbols for malar area are: N, sample size; ++, black extensive; +, black streaks broader than throat streaks; +-=, black streaks slightly broader than throat streaks; =, black streaks at rear of malar equal to throat streaks.

conditions ranging from the heavily olive-colored coverts of *C. m. melanochloros* to the white coverts of most *nattereri* and of the *melanolaimus* group. A graded series of intermediate conditions was established for the analysis, from white to slightly olive, intermediate, much olive (but not so much as in *melanochloros*), and finally the

very olive condition of *melanochloros*. There is no apparent sexual difference in this feature.

MARKINGS AT REAR OF MALAR (TABLE 2): The streaks of the throat typically blend with those of the malar stripe (in the female only) and the area posterior to the malar stripe in the *melanochloros* group. In the *melanolaimus* group

TABLE 3
ANALYSIS OF THROAT-BREAST PATCH COLOR AND COLOR OF UNDERPARTS
IN *Colaptes melanochloros*^a

Sample	Throat-Breast Color						Color of Underparts					
	N	ml	>	i	<	mc	N	ml	>	i	<	mc
<i>melanochloros</i> Group												
<i>nattereri</i> E ^b	16	0	0	1	0	15	16	5	1	4	1	5
<i>nattereri</i> W ^c	87	0	1	9	12	65	86	17	2	32	6	29
E São Paulo	4	0	0	0	0	4	4	0	0	2	0	2
Espírito Santo ^d	8	1	0	0	0	7	8	0	0	0	0	8
NW São Paulo	9	0	0	0	1	8	9	1	0	3	1	4
SE Paraguay	16	0	0	0	2	14	16	0	0	2	0	14
<i>melanochloros</i> ^e	100	1	0	0	9	90	99	0	0	1	3	95
NE R. G. do Sul	17	2	0	2	0	13	17	2	1	4	1	9
Corrientes Transects												
Ituzaingó	12	0	1	3	5	3	12	0	1	5	4	2
Ituzaingó W	3	1	2	0	0	0	3	0	2	1	0	0
Itá-Ibaté	15	2	7	4	1	1	15	7	5	3	0	0
San Carlos	6	0	2	3	0	1	6	1	0	1	0	4
Est. del Iberá	8	4	4	0	0	0	8	6	1	1	0	0
SW Corrientes	12	12	0	0	0	0	12	11	0	1	0	0
Colonia Garabí	6	0	0	0	3	3	6	0	0	1	1	4
Cuay Grande	6	0	0	2	2	2	6	0	0	0	2	4
Torrent	29	0	3	12	12	2	31	5	0	3	0	23
Alvear	5	0	0	2	1	2	5	2	0	2	0	1
<i>melanolaimus</i> Group												
Uruguay	14	10	4	0	0	0	14	8	2	4	0	0
Entre Ríos	49	46	3	0	0	0	45	38	2	5	0	0
<i>nigroviridis</i> SE ^f	42	25	12	4	1	0	41	29	6	5	1	0
<i>nigroviridis</i> NW ^g	45	30	13	1	0	1	45	16	9	20	0	0
NW Entre Ríos ^h	14	12	2	0	0	0	14	8	6	0	0	0
W Formosa	4	2	1	1	0	0	4	4	0	0	0	0
Santiago d. Estero	12	10	2	0	0	0	12	12	0	0	0	0
<i>leucofrenatus</i> ⁱ	96	93	3	0	0	0	94	87	3	4	0	0
Salta	20	20	0	0	0	0	20	12	6	2	0	0
<i>melanolaimus</i>	41	40	1	0	0	0	40	30	8	2	0	0

^a All adults are included. ^b Ceará, Piauí, Pernambuco, SE Bahia. ^c Bolivia, Mato Grosso, NW Bahia, Goiás, NW Minas Gerais, Pará, NE Paraguay. ^d Includes Rio de Janeiro. ^e Misiones, S São Paulo, S Paraná, Santa Catarina. ^f SE Formosa, E Chaco, NW Corrientes, NE Santa Fe. ^g W Paraguay, N Formosa, Villa Montes area of Bolivia. ^h Includes eastern border of Santa Fe. ⁱ W Santa Fe, Córdoba, Tucumán, Mendoza, San Luis, Buenos Aires, Río Negro, La Pampa.

Symbols: N, sample size; ml, as *melanolaimus* group; >, tending toward *melanochloros*; i, intermediate; <, tending toward *melanolaimus*; mc, as *melanochloros* group. In worn birds only ml, i, and mc may be determinable.

the malar stripe of females is blacker, and that of both sexes has behind it converging, broadly black streaks in many cases forming a solid black patch, thus differing greatly from the moderately narrow throat streaks. Thus at one extreme the postmalar streaks equal in width those of the throat; gradations are from postmalar streaks slightly broader than those of the throat, to moderately broader, to much broader, and finally to a large black area found in specimens of *C. m. leucofrenatus* and *C. m. melanolaimus*. There

is no sexual difference in the *melanolaimus* group, and none is apparent in *nattereri*, but there is a tendency for females of *C. m. melanochloros* to show broader black streaks than males.

THROAT COLOR (TABLE 3): The rear of the throat and front of the breast are washed with yellow-gold, orange, or even red-orange in flickers of the *melanolaimus* group. Within the *melanochloros* group the throat-breast area is greenish and concolored with the rest of the underparts in *C. m. melanochloros*, and generally

in *nattereri*, although some birds of the latter race do show yellow-gold throat-breast color. This feature is difficult to evaluate because of the effects of fading and wear. Generally, I disregarded the intensity of orange or gold when the patch was present. Gradations between the extremes of a fully and distinctly gold patch and absence of a patch included: (a) traces of a patch, throat-breast brighter than surrounding areas; (b) distinct but faint patch; and (c) somewhat less than full patch. In very worn birds only one intermediate condition is detectable. There is a slight tendency for males to have brighter, more orange patches than females of *C. m. melanolaimus* and *C. m. leucofrenatus*, and males of the *melanochloros* group tend to show brightening of the throat-breast area more than do females.

COLOR OF UNDERPARTS (TABLE 3): This is another character showing strong effects of wear and fading, as well as complex variation. The underparts of *C. m. melanochloros* are green, with spots uniformly distributed throughout. *Colaptes melanochloros nattereri* generally has yellower, less green underparts, in some cases tending toward white, but in others bright yellowish, and usually with reduced spotting on the abdomen. The *melanolaimus* group is variably (usually heavily) spotted and the underparts are white, often very faintly washed with yellow-green. For analysis of possible effects of hybridization I concentrated on the general background color, ignoring the spotting. Thus, white is at one extreme and green at the other; intermediate stages include white washed with green (more than that on fresh-plumaged birds), intermediate, and green pale in part (often blotchy). There was no apparent sexual difference in this feature.

TAIL BARRING: Several different measures of tail barring were taken, partly to allow evaluation of birds even when molting some tail feathers. I counted the number of bars on the inner vane of a central rectrix, the number of bars reaching the rachis from the inner vane of the outer (fifth) rectrix, and the number of bars at the outer margin of the outer rectrix. I also noted the presence or absence of barring on rectrices 2 to 4. There is great variation in tail barring, and differences exist between the various traits measured. For example, *C. m. melanochloros* has generally more bars on rectrix 5 than have specimens of the *melanolaimus* group,

but the difference in rectrices 2 to 4 is small. By far the greatest geographic variation occurs within the *melanochloros* group, between *melanochloros* and *nattereri*. Males tend to have a more barred tail than those of females, but the difference is slight.

BREAST SPOTTING: A randomly selected spot was measured on the breast of each specimen, the measurements being of greatest depth and of greatest width along the rachis. The *melanochloros* group tends to have rounder spots, and the *melanolaimus* group more transverse (barlike) spots, except for *C. m. melanolaimus*, in which the spots are streaklike. Females tend to have narrower, more rounded, less barlike spots (male samples in most cases have greater spot depth-spot width mean differences, with the width varying more than the length).

BACK BARRING: A representative dark back bar was measured on the upper back of each specimen. The bar measured is the penultimate one, which, unlike the dark bar at the tip of the feathers, rarely is affected by wear. There is great variation individually in back barring, obscuring the possible pattern of geographic variation. Females tend to have narrower bars than males, but the difference is relatively not greater than the size difference between the sexes.

GEOGRAPHIC VARIATION IN THE *MELANOCHLOROS* GROUP

The variation in this group, and the taxonomy of the forms included in "*C. melanochloros*" were discussed by Traylor (1951; see other references therein). The examination of more material than was available to Traylor convinces me that there are essentially two taxonomically recognizable groups of populations within "*melanochloros*," these being the larger forest form of southeastern Brazil, *melanochloros*, and the smaller savanna form, *nattereri*, of eastern Bolivia to Pará and Maranhão, Brazil. The other three subspecies of this group recognized by Traylor represent intergradient populations between *melanochloros* and *nattereri* ("*cris-*

tatus," "flavilumbis") or insular populations of *nattereri* ("mariae") not exceeding the range of variation in *nattereri*. Rather than discuss all of these supposed subspecies separately, I shall characterize *melanochloros* and *nattereri*, then discuss populations geographically, and finally summarize the variation encountered in populations representing the *melanochloros* group.

Colaptes melanochloros melanochloros Gmelin, 1788

Figure 2

Picus cristatus VIEILLOT, 1818 (Colonia Nueva Germania, Paraguay; see Laubmann, 1934).

DIAGNOSIS: Green above and below, generally rump concolor with back; tail moderately barred; remiges with dark pigmentation over much of the feather shafts; ear coverts mainly olive; heavily spotted below, generally throughout the underparts, the spots tending to be round, or if not round, tending to be as wide or wider than deep; barred strongly and regularly above, the dark bars being about as deep as the paler interspaces; wings long; tail very long actually, and long relative to wing length, tail/wing ratios over 0.70, and averaging 0.74 to 0.76; bill short relative to wing length and tarsal length, never longer than tarsus; tarsus moderately long (see tables 4 to 7).

RANGE: Birds diagnosed above range from southern São Paulo, and eastern and southern Paraná to Santa Catarina, in Brazil, and to Misiones, Argentina. The subspecies ranges beyond to southernmost Bahia, eastern Minas Gerais, Espírito Santo, Rio de Janeiro, western Paraná, southeastern Paraguay, the Corrientes border of Misiones, Argentina, and northern Rio Grande do Sul. Birds from the last-mentioned areas tend toward other races, but are nearer *melanochloros* than any other subspecies.

Colaptes melanochloros nattereri Malherbe, 1845

Figure 2

Picus flavilumbis SUNDEVALL, 1866 (Bahia).

Chrysomitris melanochloros juae CORY, 1919 (Ceará).

Chrysomitris mariae HARGITT, 1889 (Marajo Island, Pará).

DIAGNOSIS: Yellow-green to yellow above, paler (more yellow or even whitish) below and

on rump; tail strongly barred; remiges lacking dark pigmentation on shafts, or with slight traces to moderate amount of dark pigment; ear coverts without olive centers, white, or with small area of olive; variably spotted below, generally with spots fewer on abdomen than on breast, and spots tending to be streaklike (i.e., narrower than deep); moderately barred above, the dark bars tending to be irregular in shape (deeper at shafts tapering to less deep at edges) and light interspaces deeper than dark bars; wings short; tail short actually and relative to wing length, tail/wing ratios 0.70 or less, averaging 0.63 to 0.65; bill short, but not relative to wing length and tarsal length; tarsus short (see tables 4 to 7).

RANGE: Birds diagnosed above range from Maranhão through Goiás to Mato Grosso, and Santa Cruz, Bolivia. The subspecies ranges beyond to Piauí, Ceará, Pernambuco, western São Paulo, and eastern Bahia. Birds from these last-mentioned areas tend toward *melanochloros*, but are nearer *nattereri*. The subspecies also ranges to Marajo Island, Pará, and Mangunca Island, Maranhão (birds tend to be smaller, brighter yellow and less spotted below than birds from the area covered by the above diagnosis).

GEOGRAPHIC ANALYSIS OF VARIATION

Tables 1-7

Maranhão, Pará: Mainland Maranhão birds do not differ appreciably from Bolivian and Mato Grosso *nattereri*, although tending to have fewer spots and more streaklike spots below. Only three specimens represent "mariae" from Marajo Island, Pará (two specimens) and Mangunca Island, Maranhão (one specimen). Although the insular specimens tend to be smaller, yellower, and less marked below, they fall within the range of variation of *nattereri* in all features. Although more material may indicate that subspecific recognition is warranted for *mariae*, I do not consider it to merit such recognition because: (1) available specimens show no trenchant characters for this supposed race; (2) the separate islands involved clearly indicate that a single population is not involved; and (3) the variation shown by the insular birds is expressed best by simply recognizing tendencies for smaller size, yellower coloration and less markings in island populations at the north-

TABLE 4
ANALYSIS OF WING LENGTH AND TAIL LENGTH (IN MILLIMETERS)
OF MALE GREEN-BARRED FLICKERS^a

Sample	N	Wing Length Mean $\pm$ SE	Range	N	Tail Length Mean $\pm$ SE	Range
<i>melanochloros</i>						
N Misiones	17	147.60 $\pm$ 0.92	140–153	14	109.90 $\pm$ 1.22	101–118
S Misiones	6	145.70 $\pm$ 0.84	143–148	6	108.20 $\pm$ 1.78	103–110
Paraná	8	147.50 $\pm$ 1.31	141–152	7	109.68 $\pm$ 1.11	107–115
<i>nattereri</i>						
Bolivia-M. Grosso	7	127.43 $\pm$ 1.70	121–133	7	81.94 $\pm$ 2.52	73– 93
Goiás	(6)	128.33 $\pm$ 1.80	122–133	—	— —	— —)
Maranhão	(5)	129.60 $\pm$ 1.12	126–132	5	84.38 $\pm$ 2.92	78– 85)
NW Bahía	(10)	130.40 $\pm$ 0.74	127–133	9	94.00 $\pm$ 1.13	88–100)
NW Minas Gerais	(5)	136.20 $\pm$ 1.39	133–141	5	92.36 $\pm$ 2.22	87– 98)
NW São Paulo	5	133.00 $\pm$ 1.52	129–137	4	92.75 —	89– 95
“mariae”	(2)	— —	111–123	2	— —	71– 83)
Miscellaneous <i>melanochloros</i> Group						
SE Bahía	5	138.00 $\pm$ 1.87	132–143	5	101.60 $\pm$ 1.81	95–106
NE R. G. do Sul ^b	6	148.50 $\pm$ 1.18	145–152	6	106.50 $\pm$ 2.14	100–109
Horqueta, Paraguay	6	137.17 $\pm$ 1.19	133–142	6	93.88 $\pm$ 0.83	91– 96
C. Bado, Paraguay	5	139.80 $\pm$ 1.20	137–144	5	94.40 $\pm$ 0.93	92– 97
Riacho Negro, Par.	(4)	142.3 —	144–147	4	100.3 —	98–104)
Corrientes						
Ituzaingó	8	148.38 $\pm$ 1.60	144–158	8	102.98 $\pm$ 1.28	99–109
Itá-Ibaté	8	151.25 $\pm$ 0.75	148–154	8	101.00 $\pm$ 1.34	97–107
Est. del Iberá	5	147.40 $\pm$ 1.29	143–150	5	94.60 $\pm$ 0.81	92– 97
SW Corrientes	4	144.0 —	143–145	4	95.0 —	94– 96
Colonia Garabí	(4)	155.75 —	152–160	4	111.75 —	107–116
Torrent	(14)	148.36 $\pm$ 0.80	145–156	13	102.38 $\pm$ 1.30	93–112
<i>nigroviridis</i>						
SE Formosa	6	148.17 $\pm$ 2.14	143–154	6	96.13 $\pm$ 0.85	94– 99
Mocoví, Santa Fe	4	150.00 —	147–154	4	95.25 —	94– 97
W Paraguay ^c	9	148.89 $\pm$ 1.42	142–155	5	100.20 $\pm$ 1.50	96–104
NE Formosa	5	148.71 $\pm$ 0.68	145–152	7	96.50 $\pm$ 1.65	93–101
<i>leucofrenatus</i>						
Entre Ríos	(10)	143.20 $\pm$ 1.24	139–152	6	93.33 $\pm$ 1.33	88– 98)
Buenos Aires	10	143.40 $\pm$ 1.49	138–152	11	91.73 $\pm$ 1.47	87– 98
NW E. Ríos-E Sta. Fe	(5)	146.00 $\pm$ 1.70	142–150	5	94.10 $\pm$ 2.31	90–101)
Córdoba-W Sta. Fe	5	147.80 $\pm$ 1.46	144–152	5	95.80 $\pm$ 1.28	92–100
Tucumán	(7)	151.71 $\pm$ 1.17	146–154	7	97.86 $\pm$ 1.08	94–102)
La Pampa ^d	4	157.1 —	151–160	4	98.5 —	90–101
“patagonicus”	(7)	159.00 $\pm$ 0.69	157–162	7	104.71 $\pm$ 0.99	102–108)
<i>melanolaimus</i>						
Bolivia	17	149.14 $\pm$ 0.98	141–155	14	94.66 $\pm$ 0.87	89–104

^a Samples are of worn birds, generally September-January, except that parentheses indicate specimens used from other seasons. ^b Includes Santa Catarina. ^c Includes Villa Montes, Bolivia. ^d Includes highlands of Córdoba.

Symbols are: N, sample size; SE, standard error of mean.

eastern extreme of the geographical range of *nattereri*.

Ceará, Piauí, Pernambuco: Specimens from these states rather closely resemble *nattereri*, although tending somewhat toward *melanochlo-*

ros in size, and especially in tail/wing ratio. Inhabiting the “caatinga” (dry scrub woodland) region, they are yellower than many specimens of *nattereri*, but the latter is so variable that they are within the range of variation of *nattereri*;

TABLE 5
ANALYSIS OF BILL LENGTH AND TARSAL LENGTH (IN MILLIMETERS)
OF MALE GREEN-BARRED FLICKERS^a

Sample	N	Bill Length Mean $\pm$ SE	Range	N	Tarsal Length Mean $\pm$ SE	Range
<i>melanochloros</i>						
N Misiones	17	22.87 $\pm$ 0.25	20.3–24.3	17	26.29 $\pm$ 0.23	24.5–27.5
S Misiones	6	23.27 $\pm$ 0.45	21.4–24.3	6	26.87 $\pm$ 0.37	25.6–27.9
Paraná	8	22.84 $\pm$ 0.55	21.3–26.0	8	25.83 $\pm$ 0.22	24.8–26.8
<i>nattereri</i>						
Bolivia-M. Grosso	10	21.46 $\pm$ 0.50	19.9–23.6	10	23.04 $\pm$ 0.29	21.2–24.2
Goiás	6	20.45 $\pm$ 0.46	19.1–22.3	6	22.70 $\pm$ 0.43	21.7–24.5
Maranhão	5	20.90 $\pm$ 0.28	20.4–21.9	5	23.30 $\pm$ 0.22	22.0–24.6
NW Bahía	10	23.04 $\pm$ 0.56	20.7–26.2	10	23.31 $\pm$ 0.41	22.0–25.9
NW Minas Gerais	7	21.34 $\pm$ 0.33	19.7–22.3	7	22.88 $\pm$ 0.47	21.3–24.9
NW São Paulo	5	22.44 $\pm$ 0.53	21.0–23.7	6	23.93 $\pm$ 0.33	22.9–24.8
“mariae”	2	— —	19.0–20.0	2	— —	22.4–23.0
Miscellaneous <i>melanochloros</i> Group						
SE Bahía	6	23.33 $\pm$ 0.51	22.2–25.7	6	23.88 $\pm$ 0.26	23.1–25.0
NE R. G. do Sul ^b	6	23.15 $\pm$ 0.40	21.4–23.9	6	26.40 $\pm$ 0.47	24.8–27.7
Horqueta, Paraguay	6	22.22 $\pm$ 0.29	21.3–23.1	6	23.99 $\pm$ 0.35	22.7–25.0
C. Bado, Paraguay	5	22.50 $\pm$ 0.33	21.6–23.6	5	23.70 $\pm$ 0.44	22.5–24.7
Riacho Negro, Par.	4	22.30 —	20.9–23.8	4	24.40 —	24.0–25.1
Corrientes						
Ituzaingó	8	24.90 $\pm$ 0.50	23.0–27.2	8	26.65 $\pm$ 0.20	25.9–27.7
Itá-Ibaté	8	24.75 $\pm$ 0.27	23.8–26.0	8	27.25 $\pm$ 0.26	26.1–28.7
Est. del Iberá	5	25.78 $\pm$ 0.28	25.0–26.5	5	28.76 $\pm$ 0.22	28.3–29.5
SW Corrientes	4	25.1 —	24.4–25.8	4	28.9 —	28.6–29.1
Colonia Garabí	4	22.9 —	21.9–23.8	4	27.8 —	26.4–28.9
Torrent	17	23.60 $\pm$ 0.32	21.4–25.5	17	26.82 $\pm$ 0.22	24.0–27.9
<i>nigroviridis</i>						
SE Formosa	6	25.67 $\pm$ 0.77	22.9–28.4	6	26.67 $\pm$ 0.28	25.9–27.4
Mocoví, S. Fe	4	25.9 —	25.1–26.7	4	28.1 —	27.3–29.3
NW Corrientes	4	26.2 —	24.9–27.0	4	27.5 —	26.9–28.1
E Chaco	6	26.95 $\pm$ 0.46	25.7–28.9	6	28.20 $\pm$ 0.57	26.0–30.0
W Paraguay ^c	9	27.23 $\pm$ 0.22	26.2–28.5	9	26.94 $\pm$ 0.36	25.4–29.0
NE Formosa	6	25.58 $\pm$ 0.36	23.5–27.4	7	26.40 $\pm$ 0.29	24.0–27.8
<i>leucofrenatus</i>						
Entre Ríos	10	25.69 $\pm$ 0.27	24.5–27.0	10	27.56 $\pm$ 0.34	26.0–29.6
Buenos Aires	10	24.71 $\pm$ 0.56	21.4–28.1	11	27.31 $\pm$ 0.29	26.0–29.1
NW Entre Ríos-E S. Fe	5	25.64 $\pm$ 0.18	25.1–27.1	5	28.26 $\pm$ 0.39	27.2–29.5
Córdoba-W Santa Fe	5	29.42 $\pm$ 0.76	27.1–31.4	5	28.96 $\pm$ 0.39	27.5–29.8
Santiago del Estero	5	29.88 $\pm$ 0.52	29.0–30.4	5	29.06 $\pm$ 0.62	27.5–30.6
Tucumán	7	27.99 $\pm$ 0.29	27.3–29.6	6	29.17 $\pm$ 0.35	28.0–30.5
La Pampa	4	30.1 —	29.2–31.8	4	30.0 —	29.0–32.5
“patagonicus”	7	30.43 $\pm$ 0.43	28.8–32.0	7	29.70 $\pm$ 0.21	29.1–30.5
Salta ^d	6	27.28 $\pm$ 0.64	25.5–29.0	6	28.68 $\pm$ 0.64	26.1–30.8
<i>melanolaimus</i>						
Bolivia	12	27.29 $\pm$ 0.51	25.3–30.4	14	26.56 $\pm$ 0.32	24.3–28.4

^a Samples vary seasonally; in each case the seasonal sample is used which contains the most specimens. ^b Includes Santa Catarina. ^c Includes Villa Montes, Bolivia. ^d Highland birds only.

Symbols: N, sample size; SE standard error of mean.

TABLE 6
TAIL/WING RATIOS OF GREEN-BARRED FLICKERS^a

Sample	N	Males Mean±SE	Range	N	Females Mean±SE	Range
<i>melanochloros</i>						
N Misiones	13	74.08±0.65	71-77	13	75.77±0.53	73-79
S Misiones	6	74.17±1.34	70-78	5	74.00±0.04	73-75
Paraná	7	74.14±0.86	70-76	6	75.00±0.68	71-77
<i>nattereri</i>						
Bolivia-M. Grosso	7	64.29±1.55	57-70	7	64.71±0.75	63-69
Goiás	(4)	65.3 —	62-69	4	63.8 —	62-66)
Maranhão	(5)	63.00±1.87	61-65	—	— —	—)
NW Bahía	(9)	71.78±1.01	67-76	4	71.15 —	69-73)
NW Minas Gerais	(4)	68.5 —	66-71	—	— —	—)
Ceará	(2)	— —	70-71	4	71.8 —	70-74)
NW São Paulo	(3)	68.7 —	68-69	3	67.3 —	67-68)
"mariae"	(2)	— —	64-67	—	— —	—)
Miscellaneous <i>melanochloros</i> Group						
SE Bahía	4	72.8 —	70-74	—	— —	—
NE R. G. do Sul ^b	6	71.67±1.56	67-76	6	74.67±1.38	70-79
Horqueta, Paraguay	6	68.50±0.43	66-70	—	— —	—
C. Bado, Paraguay	5	67.60±1.08	65-71	4	66.8 —	65-69
Riacho Negro, Par.	(4)	69.0 —	67-72	—	— —	—)
Corrientes						
Ituzaingó	8	69.50±0.53	67-72	4	70.0 —	68-71
Itá-Ibaté	8	66.75±0.77	64-70	7	68.40±0.65	66-71
Est. del Iberá	5	64.00±0.50	63-66	—	— —	—
SW Corrientes	4	66.0 —	65-67	7	66.60±0.37	65-68
Colonia Garabí	(4)	72.0 —	70-74	—	— —	—)
Torrent	(17)	69.60±0.55	64-73	13	69.10±0.56	64-71)
<i>nigroviridis</i>						
SE Formosa	6	64.83±0.31	64-66	4	66.0 —	64-68
Mocoví, Santa Fe	4	63.5 —	62-66	6	65.00±1.03	62-68
NW Corrientes	4	63.3 —	61-66	8	66.80±0.90	62-70
W Paraguay ^c	6	65.67±0.80	64-68	5	64.60±1.25	62-68
NE Formosa	6	65.20±1.01	61-67	6	65.00±1.00	62-69
<i>leucofrenatus</i>						
Entre Ríos	(6)	64.00±0.26	63-64	10	65.11±0.60	62-67)
Buenos Aires	10	63.80±0.51	61-66	10	64.82±0.61	63-68
Uruguay	(—	— —	—	6	66.02±0.60	63-69)
NW E. Ríos-E S. Fe	(5)	64.20±0.86	62-67	5	64.00±0.89	62-66)
Córdoba-W S. Fe	5	64.80±0.49	64-66	5	65.61±0.93	62-67
Tucumán	(7)	64.14±0.55	63-67	8	64.00±0.42	63-66)
La Pampa ^d	4	63.00 —	60-67	5	64.40±1.03	62-68
"patagonicus"	(7)	65.86±0.46	64-67	7	64.42±0.43	63-66)
<i>melanolaimus</i>						
Bolivia	14	63.43±0.58	59-67	10	64.30±0.99	60-70

^a Samples are of worn birds except for figures in parentheses. Figures given are tail length as per cent of wing length.

^b Includes Santa Catarina. ^c Includes Villa Montes, Bolivia. ^d Includes highland Córdoba.

Symbols are: N, sample size; SE, standard error of mean.

indeed Piauihy, Ceará, and Pernambuco birds fall within the range of variation of Maranhão birds, except for their somewhat larger size and greater tail/wing ratio. They differ from the

"caatinga" birds of eastern Bahia in their smaller size, and greater degree of spotting below, hence they more closely resemble typical *nattereri* than do the eastern Bahia specimens.

TABLE 7
SOME MENSURAL FEATURES OF *Colaptes melanochloros*^a

Sample	N	Mean	Tarsus—Bill Range	Mean Breast Spot Depth	Mean Breast Spot Width	Mean Back Bar Width	Mean ^b Bars in Tail
<i>melanochloros</i>							
N Misiones	56	+3.03	+0.5 to +6.9	4.09	4.34	4.62	6.27
S Misiones	11	+3.79	+1.3 to +5.1	4.32	4.65	4.08	4.67
Paraná	14	+3.80	+1.2 to +5.5	4.13	4.08	4.35	4.63
S São Paulo	9	+3.22	+1.3 to +5.2	3.6	2.9	4.0	5.0
<i>nattereri</i>							
Bolivia-M. Grosso	25	+2.03	-0.2 to +3.7	3.54	3.53	4.16	8.39
Goiás	16	+2.05	-0.4 to +4.2	3.42	4.13	—	8.63
Maranhão	8	+2.93	+0.9 to +4.9	3.85	3.48	4.46	8.00
NW Bahía	17	+0.61	-4.2 to +2.7	3.88	3.72	3.99	7.83
NW Minas Gerais	8	+1.53	+0.1 to +3.7	3.57	4.17	3.84	7.40
Ceará ^c	10	+1.63	+0.3 to +3.2	—	—	—	8.0
NW São Paulo	9	+0.78	-0.8 to +3.8	3.68	3.85	4.10	7.80
"mariae"	3	+2.5	+0.7 to +3.4	2.8	3.1	3.5	8.0
Miscellaneous <i>melanochloros</i> Group							
SE Bahía	6	+0.55	-2.2 to +1.9	3.78	3.93	3.97	9.00
NE R. G. do Sul	23	+3.73	+0.9 to +5.3	3.58	4.15	4.03	4.91
Horqueta, Paraguay	8	+1.96	+0.5 to +3.2	4.33	4.20	4.65	5.67
C. Bado, Paraguay	9	+1.50	+0.3 to +3.1	3.60	3.62	3.92	6.40
Pto. Gibaja, Par.	13	+3.62	+2.9 to +5.8	3.98	4.05	4.65	5.13
Riacho Negro, Par.	4	+2.10	+0.2 to +3.0	3.7	—	4.5	6.3
Corrientes							
Ituzaingó	12	+1.93	0.0 to +4.5	4.31	4.72	4.96	2.50
Itá-Ibaté	14	+2.36	+0.2 to +4.0	4.13	3.80	4.71	3.75
San Carlos	6	+3.80	+2.8 to +4.8	3.9	4.4	4.8	4.0
Est. del Iberá	8	+3.07	+1.7 to +4.2	3.72	4.80	4.98	3.00
SW Corrientes	9	+3.54	+1.4 to +4.9	—	—	5.2	2.0
Colonia Garabí	6	+4.97	+3.2 to +7.0	4.5	5.4	5.1	2.3
Torrent	31	+3.38	-1.3 to +5.9	3.75	4.74	4.49	3.79
Alvear	5	+3.84	-0.1 to +5.8	—	—	—	—
<i>nigroviridis</i>							
SE Formosa	11	+1.24	-1.4 to +3.2	4.18	4.50	4.61	3.57
Mocoví, S. Fe	10	+2.18	+0.2 to +3.9	4.3	4.5	4.5	4.5
NW Corrientes	12	+1.18	+0.2 to +4.1	3.8	4.0	4.1	4.0
E Chaco	9	+1.68	-1.2 to +3.9	3.75	4.77	4.45	2.50
W Paraguay ^d	26	+0.07	-3.0 to +3.9	3.77	3.70	4.41	3.00
NE Formosa	13	+0.61	-0.5 to +3.5	4.13	4.27	4.39	3.16
<i>leucofrenatus</i>							
Entre Ríos	42	+2.06	-0.8 to +5.6	3.93	5.07	5.17	3.25
Buenos Aires	21	+2.85	+0.1 to +5.6	4.01	4.34	4.69	3.90
Uruguay	12	+2.11	-0.8 to +4.6	—	—	—	—
NW E. Ríos-E S. Fe	14	+1.96	-1.2 to +4.3	4.00	4.54	4.98	2.50
Córdoba-W S. Fe	19	+0.04	-2.1 to +3.6	4.18	5.32	4.86	1.00
Santiago del Estero	12	-0.80	-2.5 to +1.2	3.88	4.96	4.74	1.00
Tucumán	21	+1.09	-3.6 to +5.7	4.01	4.40	4.84	2.11
La Pampa ^e	10	+0.50	-2.0 to +3.1	5.0	5.4	4.5	0.8
"patagonicus"	21	-0.11	-2.8 to +2.1	4.64	4.53	5.54	0.90
Salta ^f	19	+0.69	-2.4 to +4.6	4.47	4.58	5.22	0.75
<i>melanolaimus</i>							
Bolivia	39	-0.10	-5.4 to +4.0	3.81	3.39	5.81	2.62

^a Samples used were of males, and those with the most specimens, except for Tarsus-Bill, in which all adult flickers were utilized. Measurements are in millimeters. ^b Bars touching rachis on inner vane of outer large rectrix. ^c Includes Piahy, Pernambuco. ^d Includes Villa Montes, Bolivia. ^e Includes highlands of Córdoba. ^f Highlands only.

Symbols: N, number of specimens.

Goiás: Goiás specimens are within the range of variation of Maranhão, Mato Grosso, and Bolivian *nattereri*, except for their wider, hence rounder breast spots.

Bahia: Specimens from this state are problematical, partly because of lack of adequate samples, but mainly because of apparent differentiation of a population in the arid "caatinga" region and intergradation of this population with *melanochloros* to the south, a more *nattereri*-like population to the west, and the semi-*nattereri* populations farther north (Ceará, Pernambuco). Caatinga specimens from eastern Bahia (Tambury, Baixão) are very yellow, have few spots on the abdomen, and approach *melanochloros* in size and in ratio of tail to wing length. A single specimen from the Rio Pardo in southern Bahia tends strongly toward *melanochloros* in all of its features, and best is considered assignable to that race. Thus, the zone of intergradation between the caatinga population and *melanochloros* is rather narrow near the coast, where ecological conditions probably change abruptly (nevertheless, *melanochloros* populations to the south show effects of introgression; see Espírito Santo section). Western and central highland Bahia birds approach *nattereri* in their smaller size and less yellow coloration than eastern Bahia birds; they are more heavily spotted than *nattereri*, Ceará, or eastern Bahia birds, thus tending toward *melanochloros*. The size difference between eastern Bahia and western Bahia birds is probably greater than indicated by available data because the eastern sample includes worn birds, whereas the western sample includes mainly fresh-plumaged birds. Macaco Seco and Andarahy specimens tend toward the highland birds in color, but they are like Tambury and Baixão specimens in their measurements. A Morro de Chapeo bird tends somewhat toward eastern Bahia specimens, but is small like western birds. The "Bahia trade skins" in various collections appear to come from the central highlands adjacent to the caatinga; they are small like western birds, but two of six specimens tend in color toward the caatinga birds. Northern Bahia specimens from Joãozeiro and the Rio Preto (latter actually west central Bahia) are not so similar to Ceará birds as Traylor (1951, p. 429) has suggested; they are greener, more heavily spotted on the abdomen, and larger in size. Although the tail/wing ratio approaches *melanochloros* in western and northern Bahia

flickers, these are close to *nattereri* and best are considered to represent that race. Despite their differences it should be noted that eastern and western Bahia birds are similar in their tail/wing ratios, and particularly in their bill which is long with respect to the tarsi—indeed, Bahia birds have proportionally the longest bill of any forms belonging to the *melanochloros* group. The differences between eastern and western Bahia birds are attributable perhaps to: moderate differentiation of the eastern population in the relatively uniform caatinga; great variation in the western Bahia population, which occupies ecologically more diverse habitats; and greater gene flow from savanna populations of *nattereri* into western Bahia from Goiás. *Colaptes melanochloros flavilumbis* Sundevall was described, apparently from eastern Bahia (Traylor, 1951). However, measurements of this specimen (wing 125 mm., tail 93 mm.) and its coloration (*fide* C. Vaurie; see also Gyldenstolpe, 1926, p. 75) indicate that it came from the highlands of central or western Bahia. If indeed a subspecies other than *nattereri* or *melanochloros* is recognizable in northeastern Brazil, it is apt to be the form inhabiting eastern Bahia. I do not advocate recognition of *flavilumbis* for the following reasons: (1) the rather close resemblance of eastern Bahia birds to *nattereri*; (2) the fact that traits ascribable to *flavilumbis* largely represent intermediate character states between *nattereri* and *melanochloros*; (3) the fact that traits of *flavilumbis* are much less distinctive than are those of well-defined *nattereri* and *melanochloros*; and (4) the difficulty of ascribing a geographic range for *flavilumbis*—because of its intergradation with other forms to the north, west, and south, its range would have to be restricted to eastern Bahia alone, whereas the type specimen appears to represent the population from western Bahia.

Minas Gerais: A single specimen from the southeast (São Benedicto) matches specimens from adjacent Espírito Santo, which see. The other specimens examined are from western Minas Gerais. These resemble *nattereri*, from Goiás, but tend toward *melanochloros* in size and in their greener coloration; they also generally resemble specimens from northeastern Paraguay, western Bahia, and Ceará. The tail/wing ratio is near that of *nattereri*, not that of *melanochloros* or of the Bahia birds. In bill length and its relation to tarsal length, birds from western

Minas Gerais resemble those of the sample from Ceará and Pernambuco (these in turn are intermediate between *nattereri* and birds from Bahia).

Rio de Janeiro, Espírito Santo: These birds of the humid coast closely approach *melanochloros*. They differ in having a paler rump, and especially in having less dark pigment in the remiges; they also tend to have a longer bill than *melanochloros* specimens from farther south, and to be slightly smaller. These differences from *melanochloros* represent tendencies in the direction of *nattereri*, which occurs in adjacent Bahia. Hence, they are likely to be due to introgression.

São Paulo: Birds from southern São Paulo are typical of *melanochloros*. Four birds from eastern São Paulo (Victoria, Bebedouro, Rincão) generally resemble *melanochloros* but they are very small (wing 135 to 143 mm., tail 92 to 103 mm.), they have lower tail/wing ratios (0.68 to 0.76), and they tend to have less (even none in two birds) dark pigment in the remiges and ear coverts. These differences from *melanochloros* represent tendencies toward *nattereri*, but the specimens are assigned to *melanochloros* for the present. Birds from near the Parana River in western São Paulo strongly tend toward *nattereri* in ventral and rump coloration, reduced dark pigment in the remiges, more barred tail, paler ear coverts, much shorter wings, tail and tarsi, and in tail/wing ratio. These birds have been assigned to "*cristatus*" (Traylor, 1951), which I do not recognize because this supposed subspecies actually represents clinally variable populations intermediate between, and located between the ranges of *nattereri* and *melanochloros*.

Paraná: Fifteen specimens from Paraná are typical of *melanochloros*, except for one specimen, that being the only one from far western Paraná (Parana River). The latter very closely approaches *nattereri* in overall coloration, the paleness of its rump and the lack of dark pigment in the remiges, and lack of olive in the ear coverts; it has a short tail (96.5 mm.) as well (wing molting, and bill broken, hence not measurable).

Mato Grosso: These specimens are typical of *nattereri*, except for São Francisco, Campo Grande, and Vaccaria (southern, southeastern Mato Grosso) birds which tend toward *melanochloros* in size, ventral spotting, and overall coloration.

Eastern Paraguay: The situation in eastern Paraguay is complex because of the influence from *melanolaimus* group populations west of the

Paraguay River, and probably in the southwestern corner of eastern Paraguay. Specimens from the Parana River from Encarnación east and north, and westward from the river as far as Caaguazú and Villa Rica are close to *melanochloros* in size and coloration, although showing some tendencies toward *nattereri*. Toward the north (Capitán Bado) and west (localities just east of the Paraguay River) *nattereri* influence increases, apparently clinally (more specimens are needed to clarify the picture). The situation in eastern Paraguay, as well as those in Misiones and Rio Grande do Sul, where influence from "*melanolaimus*" populations is evident, are discussed more fully below.

SUMMARY OF VARIATION WITHIN THE *melanochloros* GROUP

Variation within this group is great, exceeding that found in the *melanolaimus* group (which see). Certainly there has been partial, effective isolation of certain populations (northeastern Brazil), and probably even full geographic isolation of *nattereri* and *melanochloros* (possibly during glaciation). Interbreeding of these two races in a secondary contact of variable age along its extent, and with local variation in the nature of the contact, would explain much of the observed variation. So, too, does the fact that intergradation occurs in ecotonal savanna-forest areas, where intermediate populations may develop and exhibit great individual variation. I view *nattereri* as a savanna derivative, and *melanochloros* as a subtropical forest derivative. From this it is expected that ecotonal, interdigitating forest-savanna areas such as eastern Paraguay would contain variably intermediate populations. Finally, according to this view selection ought to be more similar between *nattereri* and the *melanolaimus* group than between *melanochloros* and the *melanolaimus* group, for the savanna, woodland edge, and caatinga habitats of *nattereri* resemble the habitats (pampas edge, chaco woodland, scrub woodland) favored by the *melanolaimus* group. This ecological similarity between *nattereri* and the *melanolaimus* group also may favor greater introgression from the latter into *nattereri* populations than into *melanochloros* populations. In any event *nattereri* resembles the *melanolaimus* group morphologically to a greater extent than does *melanochloros*.

The race *melanochloros* is larger in size (apparent from skins, no weights available for *nattereri*), and shows greater wing length, much greater tail length, greater tarsal length, somewhat greater bill length, and a darker, greener coloration than *nattereri* (see diagnoses above for other features). This race inhabits the area from northern Rio Grande do Sul north to São Paulo and beyond (somewhat intergradient toward *nattereri*) to southernmost Bahia, and west to western São Paulo, western Paraná, Misiones, and the southeastern edge of Paraguay. Intergradation with *nattereri* occurs around the entire northern and northwestern periphery of this range from east-central and northeastern Paraguay, southeasternmost Mato Grosso, the western edge of Paraná, northwestern São Paulo, most of Minas Gerais, and western Bahia. The zone of intergradation varies in width (see discussion of factors above), and it remains to be defined clearly in much of the region of its occurrence.

The smaller, paler, yellower, and less heavily marked *nattereri*, with its proportionally short tail occupies the area from lowland Santa Cruz, Bolivia east across Mato Grosso to Goiás, and beyond to Maranhão and islands off the coast north to Marajó, Pará. Insular populations contain birds of small size. From this campo area, *nattereri* swings southward and eastward into the caatinga region through Piauí and Ceará to Pernambuco, and southward to east-central Bahia. The population of this region contains birds with tails proportionally intermediate between those of *melanochloros* and *nattereri*, and these flickers tend to be larger than *nattereri*, but they are close to it in coloration and hence are assigned to *nattereri*. Intergradation with *melanochloros* occurs in the region noted above.

GEOGRAPHIC VARIATION IN THE *MELANOLAIMUS* GROUP

Geographic variation in this group is considerably less than in the *melanochloros* group, and no population of the *melanolaimus* group approaches the level of differentiation of *C. m. nattereri* or *C. m. melanochloros* of the *melanochloros* group. Nevertheless, as many as five subspecies have

been recognized (Traylor, 1951) within the *melanolaimus* group. Among the described races, *melanolaimus* and *nigroviridis* appear by virtue of their attributes and distribution to merit recognition; the less distinct *perplexus*, and the even less distinct *patagonicus* seem best merged within *leucofrenatus*. There follow diagnoses of the subspecies which I recognize, consideration of samples by area, and finally a summary of variation in this group.

Colaptes melanochloros melanolaimus Malherbe,
1857

Figure 2

DIAGNOSIS: The fundamental feature of this race is its black throat with reduced white markings (this is the only race of *melanochloros* thus resembling *C. punctigula*); rump white, spotting reduced; tail least barred among races of the *melanolaimus* group; rear of malar region black and extensive, merging with black of throat (80 per cent separable from 76 per cent of all other specimens representing the *melanolaimus* group); tend to have more greenish yellow traces below than *leucofrenatus*, fewer traces than *nigroviridis*; spots below tend to be streaklike (61 per cent show spots distinctly deeper than wide, vs. 25 per cent of specimens from elsewhere); back bars very broad, but great overlap with other races; and mensural characters not diagnostic, although tending to have relatively longer bill (bill longer than tarsus in more than half the specimens; see tables 4 to 7).

RANGE: Bolivian highlands (Cochabamba, western Santa Cruz, Sucre, Potosi, western Tarija), intergrading with *leucofrenatus* to the south and probably with *nigroviridis* to the southeast.

Colaptes melanochloros nigroviridis Grant, 1911

DIAGNOSIS: More than half the specimens (52 to 84 per cent in various samples) show some to strong greenish coloration above (also more than other races it tends to be greener below); rump greener, less white, more heavily spotted than other races (especially *melanolaimus*); more

barred tail than other races (approached by eastern populations of *leucofrenatus*); less black in throat than other races; rear of malar region with black streaks not greatly broader than streaks on throat (65 per cent have less black than 86 per cent of specimens of other races), hence tends to lack the black "mark" behind the malar otherwise typical of the *melanolaimus* group; reduced orange-yellow on anterior breast and rear of throat; tends to have narrower back bars than other races; and mensural characters nondiagnostic (resembles *melanolaimus* and eastern *leucofrenatus* generally; see tables 4 to 7).

RANGE: Paraguay west of the Paraguay River, Bolivia in easternmost Tarija (Villa Montes), and northern and eastern Formosa, eastern Chaco, the northwestern corner of Corrientes and northeastern Santa Fe, Argentina. Probably interbreeds with *C. m. nattereri* in northernmost Paraguay and possibly in southern Santa Cruz, Bolivia, and southwestern Mato Grosso, and with *C. m. nattereri-melanochloros* sporadically across or along the Paraguay River (see *C. m. melanolaimus* and *C. m. leucofrenatus* for intergradation with those races.)

Colaptes melanochloros leucofrenatus Leybold, 1873

Figure 2

Chrysophilus melanolaimus perplexus CORY, 1919 (Buenos Aires, Argentina).

Chrysophilus melanolaimus patagonicus LAUBMANN, 1934 (Neuquén, Argentina).

DIAGNOSIS: Throat and rear of malar less black than in *melanolaimus*, more black (broader black streaks, merging at rear of malar) than in *nigroviridis*; otherwise resembles *melanolaimus* in coloration, but tends to have more barred tail, more spotted rump, rounder spots below, and narrower bars above; mensural features nondiagnostic.

RANGE: Uruguay, and Argentina in Entre Ríos, northern Buenos Aires, southern Santa Fe, Córdoba, Santiago del Estero, Tucumán, Mendoza, San Juan, La Pampa, eastern Neuquén, northern Río Negro, and southern and southwestern Buenos Aires. Interbreeds with *melanochloros* in Rio Grande do Sul, Brazil, and eastern Corrientes, Argentina, and intergrades with other races of the *melanolaimus* group in Corrientes, Santa Fe, northwestern Entre Ríos,

western Formosa, Salta, and probably Jujuy, Argentina.

ANALYSIS OF GEOGRAPHIC VARIATION

Tables 1-7

Salta and Jujuy: No specimens were examined from Jujuy. All Salta specimens (N=20 adults, one juvenile) came from western and southwestern Salta, that is within and adjacent to the highlands; none came from lowland northeastern Salta¹ where tendencies toward *nigroviridis* might be expected. Examination of the available specimens showed no differences between "lowland" specimens (from Lerma Valley, Salta, and Cerro Colorado, Metán, all at elevations from 1000 m. to 1500 m.) and "highland" specimens (e.g., Río Escoipe, Cachi, mountains above Rosario de Lerma), which were therefore considered together. The specimens were variously intermediate between *melanolaimus* and Tucumán specimens of *leucofrenatus*. They tend toward *leucofrenatus* in the preponderance of features, and especially in having a less black throat, less black rear of the malar, and rounder, less deep spots on the underparts than *melanolaimus*. Nevertheless they show intermediacy in amount of tail barring, bill length, tarsal length, and in having blacker throats and more black in the malar region than do specimens from various samples of *leucofrenatus*. Therefore, I consider them to represent intergrade specimens, *C. melanochloros leucofrenatus* > *melanolaimus*.

Santiago del Estero and western Formosa: The small sample of specimens from Santiago del Estero represents but three localities in this large province. Furthermore all but two of the 12 specimens available to me were taken from April to July, and these include several very large specimens possibly representing migrant birds from the south (Cordoban highlands, possibly La Pampa). Among the large specimens are males with wings measuring 156 mm. and 157 mm., a female with a wing length of 160 mm. and tail length of 112 mm. The latter (unnumbered, in the Argentine National Mus-

¹Five specimens from Orán, in lowland northern Salta, were examined after the studies were completed. They prove to resemble *nigroviridis* closely, but show tendencies toward *leucofrenatus*. There is no *melanolaimus* influence, and they do not resemble highland Salta birds very closely.

eum, from Sancho Corral, Santiago del Estero) exceeds all other specimens of the *melanolaimus* group in tail length. In contrast, September specimens from Colonia Dora measure 145 mm. and 149 mm. in wing length and 95 mm. and 98 mm. in tail length (male and female, respectively). Whether or not migrant birds are present in the sample, the specimens comprising the sample do not approach *nigroviridis*, except for having less black at the rear of the malar than is found in *leucofrenatus*. The Santiago del Estero specimens closely resemble *leucofrenatus* (no green above or below, tail barring, strong orange on throat, long bill, and long tarsi), but in wing length and in tail length their measurements average greater than in those of surrounding areas, including *leucofrenatus* (Córdoba, Tucumán, also Salta birds) and *nigroviridis* (Chaco, Formosa, Paraguay). Four specimens from western Formosa (Ingeniero Juárez) cannot so readily be assigned to subspecies. These specimens mensurally resemble *nigroviridis* (especially in fairly short bill, tarsi, and wings), and two of them have reduced orange on the throat and breast, but in color of underparts and upperparts, they are like *leucofrenatus*. I consider them intergrades nearest *nigroviridis*, that is *C. melanochloros nigroviridis* > *leucofrenatus*.

Santa Fe and eastern Córdoba: Unfortunately few specimens were available from Santa Fe. The specimens represent the western border region (three from Ceres, in Santa Fe, and five from Bell Ville and Leones just to the west inside Córdoba), the eastern border region (along the Parana River, centering about Santa Fe, four specimens, and also eight from along that river on the Entre Ríos side), and the northern part of Santa Fe (Mocoví-Ocampo region, 10 specimens). The birds from the western border region resemble *leucofrenatus* in most features, especially in their strongly orange breast and the considerable black on the throat and at the rear of the malar region. Like western populations of that race, they have long bills and long tarsi. They show tendencies toward *nigroviridis* in having traces of green above and below (three specimens), and in having quite spotted, somewhat greenish rumps. Specimens from the eastern border also tend toward *leucofrenatus*, and particularly toward southeastern populations of that race in back color, strong back barring, and wing length and tail length. Probably because of the continuous contact

available with *nigroviridis* along the Parana River, the eastern sample shows somewhat more influence of *nigroviridis* than do the western specimens. In particular, I note the yellow-green traces in the underparts of six specimens, and their relatively long bills. Central and southern Santa Fe have been modified greatly by man, perhaps severely limiting contact between populations along the Parana River and those in scrub woodland at the western edge of Santa Fe. The sample from Mocoví and Ocampo is essentially *nigroviridis*, but tendencies toward *leucofrenatus* are evident in their clearer, whiter rumps, their relatively orange breasts, and their long tarsi (long tarsi tend toward western *leucofrenatus*).

Northern Entre Ríos and southwestern Corrientes: Available from southwestern Corrientes were 12 specimens, representing two localities (Concepción, Mercedes) situated well inland to the east of the Parana River. Wooded habitats at these two localities probably are somewhat tenuously connected with woodlands along that river. Ten specimens from northwestern Entre Ríos were examined. These represented localities near or along the Parana River (Viale near Paraná, and Santa Elena, represented by one and seven specimens, respectively), except for two specimens from San José de Feliciano which is in dry, chaco-like woods to the east of the river. Samples from both areas approach *leucofrenatus* from southern Entre Ríos more than they resemble *nigroviridis*. Of the two samples, the northwestern Entre Ríos birds exhibit slightly more *nigroviridis* influence than do specimens from southwestern Corrientes. Their tarsi and bills average longer than those of the Corrientes birds, they show more green in their plumage, and two specimens have reduced orange on their breasts (all the southwestern Corrientes specimens are orange-breasted). These tendencies probably reflect the greater accessibility to gene flow from *nigroviridis* of the population along the Parana River, compared with populations situated more inland (to the east). The Corrientes birds show considerable tail barring, and seven of the 12 birds in that sample have breast spots distinctly deeper than broad—this condition is typical of *melanolaimus*, and to a lesser extent of western Argentine *leucofrenatus*. Specimens in both samples clearly approach *leucofrenatus* in most characters, and they best are considered to represent that subspecies. The

center of the area of intergradation between *leucofrenatus* and *nigroviridis* in this region must occur between Reconquista, Santa Fe, and the Entre Ríos-Corrientes border along the Parana River, and west and north of Concepción east of the Parana River in Corrientes.

Northern Buenos Aires, Entre Ríos, Uruguay, and the "*perplexus*" problem: Samples from northern Buenos Aires and from Entre Ríos are similar, although the latter shows more influence of *nigroviridis* (and of *melanochloros*, see below). In certain respects the Buenos Aires-Entre Ríos birds tend to differ from western Argentine *leucofrenatus* in the same way as *nigroviridis*, perhaps because of similar selective factors operating in the more eastern areas. These tendencies include a more barred tail (although not so much as in *nigroviridis*), and a short bill and short tarsi. However, these tendencies are slight; as Traylor has noted (1951, p. 434), "this race (= '*perplexus*') is practically a small version of *leucofrenatus*," which it resembles very closely in coloration. Recognition of *perplexus* for the Buenos Aires-Entre Ríos birds would have to be on the basis of small size. Indeed, the wings, tail, and bill are significantly shorter than those of birds from say, Tucumán. There is considerable overlap between birds in these samples however (and even more between Buenos Aires and Córdoba birds), and in any case the differences (4 to 5 mm. wing length, 3 to 4 mm. tail length, 2 to 3 mm. in bill length) seem too small to warrant subspecific recognition of *perplexus*. As noted above, contact between eastern and western *leucofrenatus* populations is limited in the north (Santa Fe), although intergradation with *nigroviridis* appears to occur in Corrientes and probably occurs in north-central Santa Fe. The southeastern *leucofrenatus* populations also appear rather disjunct from western *leucofrenatus* populations in western and southern Buenos Aires. There probably are three reasons for this. First, the eastern populations occur in woods and woodland edges, and these principally are found along the rivers and streams about the La Plata delta, the great Uruguay and Parana rivers, and the coastal regions. Second, western *leucofrenatus* populations occur in chaco scrub woodland and this habitat is remote from the eastern Buenos Aires woodlands. Lastly, removal of native trees and entire woodlands (and their replacement by relatively sterile eucalyptus groves) by man doubtless has tended to restrict,

perhaps severely, the contact of eastern riparian and isolated woodland grove populations with those of the dry woodlands to the west. Hence, the isolation of the eastern populations may be much greater now than in the recent past. This isolation seems to be fractionating the eastern populations as well. For example, woodlands have been eliminated from much of the Uruguay River in Entre Ríos and Uruguay, so that Uruguayan populations are virtually disjunct from those in Entre Ríos and Buenos Aires. In any event, Uruguayan birds, although resembling those from Entre Ríos and Buenos Aires, show definite differences, most of which can be ascribed to introgression from *melanochloros* in Rio Grande do Sul. Nevertheless, Uruguay specimens clearly should be assigned to *leucofrenatus* (specimens from the Rio Grande do Sul-Uruguay border are nearer *leucofrenatus* than *melanochloros*, hence all Uruguay birds are assignable to the former race). Introgression as it affects the Uruguay birds is discussed below.

Córdoba, La Pampa, and the "*patagonicus*" problem: The population occupying scrub woodlands and riparian woods in Neuquén and northern Río Negro is in contact with the population of northern Córdoba and Tucumán through populations occupying the arid scrub (low "chaco" woodland) that extends from southern Buenos Aires and northern Río Negro in an arc northwestward through westernmost Buenos Aires and La Pampa to Córdoba. The population inhabiting the mountains of Córdoba resembles birds from La Pampa rather than lowland Córdoba specimens. The Neuquén-Río Negro birds, sometimes including those from La Pampa, have been considered racially distinct from northern birds (Laubmann, 1934; see Traylor, 1951). This race, "*patagonicus*," like "*perplexus*" must be defined by size characters if it is to be recognized, for it differs not at all in coloration from *leucofrenatus* from Córdoba and Tucumán. These birds (Neuquén, Río Negro, southwestern Buenos Aires) are the largest (see fig. 2) of this species, approximating *Colaptes campestris* in wing length and weight. They average over 30 grams heavier than eastern *leucofrenatus*, *nigroviridis*, or *melanolaemus* specimens, and although weights are unavailable from Tucumán and Córdoba specimens, they appear to exceed them somewhat as well. The mensural differences are of the order of 8 mm. for wing length, 6 to 7 mm. for tail length, 2 to 3 mm. for

bill length (differences between Tucumán and Río Negro samples in these three mensural characters in both sexes are highly significant according to Student's T test analysis), and about 1 mm. for tarsal length, with the southern birds having the greater measurements. There is almost no overlap in wing length (see below), moderate overlap in tail length, considerable overlap in bill length, and great overlap in tarsal length between Tucumán or lowland Córdoba and Río Negro birds. Greater overlap occurs between Tucumán-lowland Córdoba and highland Córdoba-La Pampa birds, although these barely show overlap in wing length. There is evidence that the southern birds are partly migratory (see Santiago del Estero discussion above). For example, the following are measurements of birds (representing all seasons) from Tapia, Tucumán: wing length—male 148 mm., four females 146 to 157 mm.; and tail length—male 94 mm., four females 93 to 99 mm. Another male, taken in June (=winter) at the same locality measures 161 mm. in wing length and 108 mm. in tail length. The last bird may represent a migrant from highland Córdoba or from farther south. If birds such as this and the Santiago del Estero specimen are not migrants, then occasional birds from throughout the western range of *leucofrenatus* may attain the wing length and tail length typical of the southern birds. Pergolani de Costa (1944, p. 362) cited an October specimen from Neuquén (western possibly; eastern Neuquén is listed by her as within the range of "*patagonicus*") with a wing length of 152 mm. as having "characters of *leucofrenatus* more than of *patagonicus*." I do not think that *patagonicus* is worthy of subspecific recognition because: (1) it is identical with *leucofrenatus* in features other than a few mensural characters, and hence does not approach the level of differentiation of *melanolaimus* or *nigroviridis*; and (2) it overlaps with *leucofrenatus* to some extent even in its trenchant character, wing length, as well as in other mensural features. Rather than assigning a trinomen to this southern population of *leucofrenatus*, it seems more appropriate to state simply that birds of the southern population tend to have somewhat longer wings, tails, and bills than northern birds. There is a direct contact between southern and northern populations, and it is likely that the variation observed will prove clinal when specimens become available from northwestern La

Pampa, southern Córdoba, and the foothills of the Sierra de la Córdoba, southern San Luis and southeastern Mendoza. On the contrary, there is no evidence for existence of a contact between large-sized birds of the chaco scrub population of southernmost Buenos Aires Province, and the small-sized birds of northern Buenos Aires.

SUMMARY OF VARIATION WITHIN THE *melanolaimus* GROUP

Variation among populations of this group is not very great; indeed some taxonomists may prefer to recognize only one subspecies, *melanolaimus*, for the entire group. The populations occupying a great arc from Uruguay, Buenos Aires, and northeastern Río Negro west and north to the highlands of Bolivia are comprised of birds similar in general coloration, especially as individual variation in spotting, streaking, tail barring, and rump color is considerable. Among these populations only the black throat and streaklike ventral spots of Bolivian *melanolaimus* stand out as marked departures in coloration. In contrast, the populations of the northern and eastern Chaco from Paraguay to northwestern Corrientes and northern Santa Fe (*nigroviridis*) are greener, less orange on the breast, less black on the throat and at the rear of the malars, and more strongly barred than other populations of this group. These and other features of *nigroviridis* represent tendencies toward the *melanochloros* group, and they may be the result of introgression.

In various mensural traits the picture is different. Certain east-west shifts occur, notably an increase in bill length westwardly. However, there are no clear-cut north-south clinal shifts. Rather, birds from Bolivia (*melanolaimus*), western Paraguay (*nigroviridis*), Tucumán (*leucofrenatus*), and Uruguay (*leucofrenatus*) approximate each other in weight, and in tarsal length; the southeastern samples (from Uruguay, Entre Ríos, northern Buenos Aires) contain shorter-winged, somewhat shorter-tailed and somewhat shorter-billed birds. In contrast to the lesser measurements of southeastern compared with northern flickers, those from the south have longer wings, tails, and bills and they weigh 20 to 25 per cent more than northern and southeastern birds. No smooth clines exist, for the shifts to the southeast and to the south occur over a rather short distance, respectively in

Santa Fe and Corrientes, and in southern Córdoba and probably southeastern Mendoza and southern San Juan. Various factors can be advanced to at least partly explain this variation. Such factors include: (1) *nigroviridis* inhabits warmer, more forested areas, perhaps forages more arboreally; since it is adjacent to the range of the *melanochloros* group, similar environmental factors and interbreeding may be responsible for its component genotypes and phenotypes; (2) western and southern populations occupy cooler, less wooded areas; flickers of these populations may feed more terrestrially (hence longer bills, whiter rumps possibly selected for); (3) isolation of *melanolaimus* in Bolivia, and of the southeastern *leucofrenatus* populations in Buenos Aires, Entre Ríos and Uruguay, have favored differentiation; (4) occupation of colder, southern areas and possibly the assumption of winter-wandering or even semi-migratory habits may be responsible for the large size and greater measurements of the southern birds; and (5) populations in proximity to the *melanochloros* group probably are affected by introgression from that group of populations; affected may be *melanolaimus* (slightly), *nigroviridis* (see 1 above), and southern Corrientes, Entre Ríos, and Uruguayan populations of *leucofrenatus*.

THE CORRIENTES TRANSECTS

The province of Corrientes, Argentina, is critical for contact between populations of the *melanochloros* and *melanolaimus* groups of Green-barred Flickers. Traylor (1951) had no specimen from this province, and his map indicates that flickers did not occur in Corrientes. In fact, all wooded areas of that province are inhabited by these birds, and the two major river valleys (Uruguay, Upper Parana, and Lower Parana) afford more or less continuous flicker habitat. Through the efforts of William Partridge, and my own activities a series of 103 adult specimens is now available from various parts of Corrientes, providing important material for an evaluation of the interactions of the two forms of Green-barred Flickers. These specimens are discussed

below under three different transects, for reasons that I shall present.

THE EASTERN CORRIENTES TRANSECT

Habitat supporting Green-barred Flickers occurs in the form of riparian forest along the Uruguay River, and in isolated patches of "monte" woodland back from the river. Formerly this riparian forest was continuous along the Uruguay River to its delta, but it is now severely limited in extent and discontinuous because of the cutting of trees. Vast stretches of riverbank (both sides of the river) are treeless, especially from southern Corrientes south through Entre Ríos. In former times, at least, the riparian woodland afforded a direct contact between populations of the *melanochloros* group (*C. m. melanochloros*) centered in the subtropical forests of Misiones, and the pampas woodland population of the *melanolaimus* group (*C. m. leucofrenatus*) inhabiting eastern Entre Ríos. Collections made by Partridge and his associates (including Kenneth C. Parkes and Philip S. Humphrey) in 1962, and by Richard S. Crossin and me in 1967 produced 48 adult specimens from the Uruguay River region of eastern Corrientes. These specimens essentially represent four localities (see map, fig. 3), namely: (1) Colonia Garabí (including Garruchos and Estancia Rincón de las Mercedes) situated from 3 to 15 miles south of the Misiones-Corrientes border; (2) Cuay Grande, 37 miles to the south of Colonia Garabí; (3) Torrent, 15 miles south of Cuay Grande; and (4) Alvear, 18 miles south of Torrent. Comparisons were made with samples of *C. m. melanochloros* from Paraná-Santa Catarina (N=20), northern Misiones (N=65), and southern Misiones (N=11), and samples of *C. m. leucofrenatus* from Entre Ríos (N=51, including two specimens from Uruguaiana, Rio Grande do Sul, situated across from southeastern Corrientes that is, about 60 miles south of Alvear), and from Buenos Aires (N=24). For the purposes of discussion in this section, *melanochloros* and *leucofrenatus* are used to indicate the samples just described, unless otherwise stated.

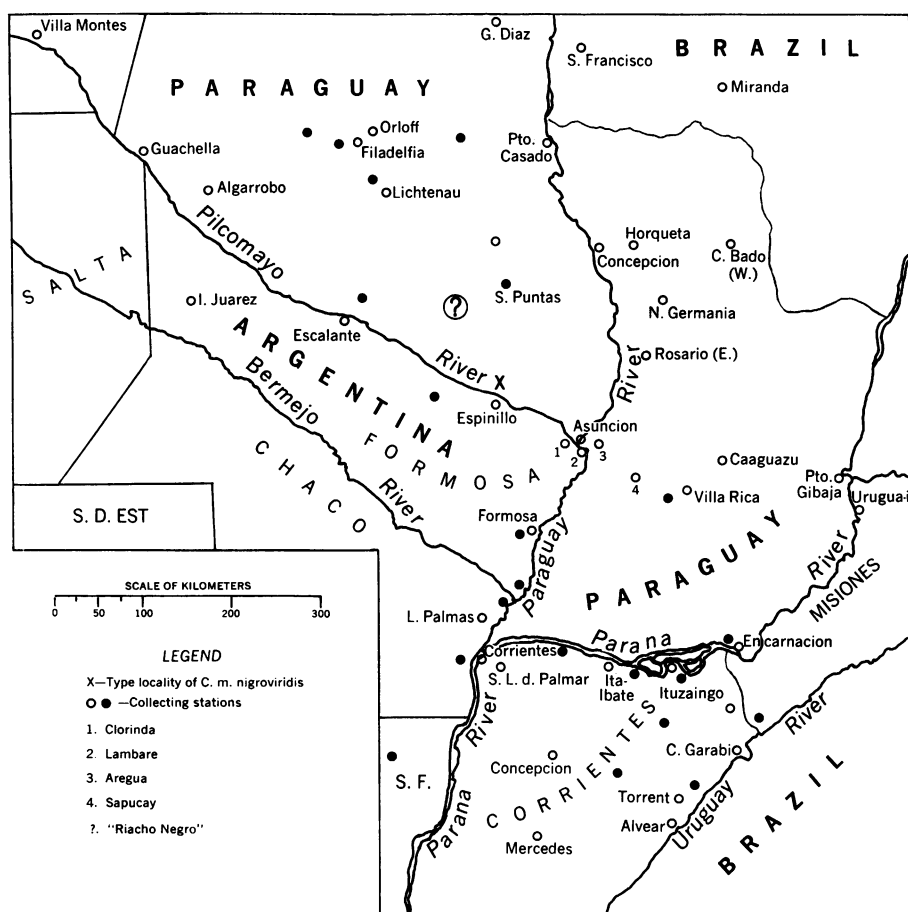


FIG. 3. Collecting stations of specimens of *Colaptes melanochloros* in northeastern Argentina-Paraguay region (see text). Not all Misiones localities are shown. Black spots represent stations away from major towns. Samples were comprised of one of more specimens. Shown in Misiones is major collecting station, Uruguai, of the late William Partridge. Many localities on the map also are collection sites of *C. campestris* (see text).

COLONIA GARABÍ

Tables 1-7

The six birds from this locality closely resemble Misiones specimens of *C. m. melanochloros*, but despite the small sample size, tendencies toward *leucofrenatus* are evident. These tendencies are most apparent in color of the remiges, ear coverts, rear of throat, and underparts, and in tarsal length. To a lesser extent they seem to involve rump color, the amount of black at the rear of the malar, and the tail/wing ratio.

All six specimens have at least somewhat reduced melanic pigment in the remiges (only 40 per cent of *melanochloros* specimens show some

pigment reduction), and one has but traces present. Although differing markedly from northern Misiones specimens in this trait, the Colonia Garabí sample resembles that of southern Misiones in the reduction of pigmentation, which represents a tendency toward the *melanolaimus* group (table 2). One of the six specimens is like *leucofrenatus* in ear covert color (white, table 1), exceeding the variation in all specimens of *melanochloros*. Half of the six specimens show traces of gold in the rear of the throat-anterior breast region, compared with but 10 per cent of Misiones and Paraná specimens (table 3). Two specimens tend toward *leucofrenatus* in color of underparts (table 3; only

three of 90 *melanochloros* do so). All six specimens from Colonia Garabí exceed the average tarsal length for *melanochloros*; three have measurements exceeding those of all 91 specimens from Misiones, Paraná and Santa Catarina. Pale rumps of four specimens, wider black post-malar streaks in three birds, and tail/wing ratios of 0.70 to 0.72 in three (of five) specimens also suggest tendencies toward *leucofrenatus*. The Colonia Garabí sample is peculiar in that wings of the males are very long. All four males exceed *melanochloros* in wing length, and three exceed Buenos Aires and Entre Ríos specimens of *leucofrenatus* as well. The cause of this variation is unknown (possibly heterosis; see discussion of other samples).

CUAY GRANDE

Six specimens from this locality resemble those from Torrent (see below), but they tend somewhat more toward *melanochloros* in ear covert color, color of underparts, black on rear of malar, tail length, and tail/wing ratio. Overall, the birds are closer to *melanochloros* than to *leucofrenatus*, but they show much more influence of the latter than do Colonia Garabí flickers. Three of the six specimens have paler, browner back color than typical of *melanochloros*, and two of these exceed variation in *melanochloros*, and in birds from Colonia Garabí. All the birds have the rump paler than the back. None of the Cuay Grande specimens has extensive dark coloring in the primary shafts, and only one has a fair amount of dark coloring. Indeed two specimens show not even traces of dark pigmentation (the other three show traces only). One specimen has fully white ear coverts (= *leucofrenatus*), although the other birds are *melanochloros*-like. Four of the six specimens exhibit some orange-gold in the breast-throat area, and two of these have a considerable amount of this coloring, although not closely approaching *leucofrenatus* in extent and intensity. Two specimens have pale, whiter underparts than most *melanochloros*. Three birds have a bill length exceeding that of *melanochloros*, whereas one specimen is shorter-billed than *leucofrenatus* specimens from farther south. Two specimens likewise exceed *melanochloros* in tarsal length, and the ranges of variation for both sexes fall within those of *leucofrenatus*. The tail/wing ratios fall within the range of *melanochloros*, but all six are at the low extreme (range 0.70 to 0.71). One male and two females exceed both

melanochloros and *leucofrenatus* in wing length, a phenomenon found in the hybrid populations.

TORRENT

Tables 1-7

The 31 specimens from Torrent comprise the major sample from the region of interbreeding within this transect. These specimens resemble *melanochloros* generally somewhat more than *leucofrenatus*, but they clearly represent a hybrid population. In character after character they are more or less intermediate, often bridging the gap between the two forms. In back color they tend toward *melanochloros*, but well over half (21 of 31) are not so green as *melanochloros*, and four intermediates exceed the variation in *melanochloros*. Barely over half of the specimens (16) have the rump concolored with the back, and one specimen has the whitish rump typical of *leucofrenatus*; the specimens present the entire spectrum of rump coloration found in the samples of *melanochloros* and *leucofrenatus*. The birds average less barring in the tail, falling within the range of *leucofrenatus* more closely than that of *melanochloros*; two specimens lack barring on the inner vane of the outer (fifth) rectrix, a condition not found in *melanochloros*. In the coloration of the shafts of the remiges, 10 birds have moderate (dark) pigmentation, 13 have but traces and eight lack pigment. The number of birds showing pigmentation and the amount of it that is present far exceed that observed in *leucofrenatus*, but two-thirds of the birds exceed the variation found in *melanochloros*. There is hence intermediacy in this trait. Unfortunately data were lost for the male specimens in this sample (specimens in Buenos Aires), but the 17 females completely bridge the gap between fully white (*leucofrenatus*) and fully olive-marked (*melanochloros*) ear coverts. Seven specimens exceed the range of variation found in *leucofrenatus*, whereas 10 fall outside the range of *melanochloros*. In the amount of black in the streaks at the rear of the malar, an approach to *melanochloros* is evident, although nearly as many birds have blacker streaks behind the malar as those whose streaks there match the throat streaks in their blackness (12 of 31 have distinctly blacker streaks behind the malar than on the throat, four have subequal streaks, and 15 have streaks the same in both areas). The trend in throat (anterior breast) color also is toward *melanochloros*; 12 birds are

intermediate, only three tend toward *leucofrenatus*, 12 toward *melanochloros*, and two are like *melanochloros* in lacking traces of orange-gold. Nevertheless, the presence of some orange-gold color on 29 of 31 specimens clearly indicates that there is gene flow from *leucofrenatus*. The underparts of most birds match those of *melanochloros*, but several specimens are intermediate and five approach or attain the condition found in *leucofrenatus* (note that all specimens are in fresh plumage, hence at their greenest below; worn birds would doubtless show more influence of *leucofrenatus*). In any case the sample bridges the conditions found in these two subspecies.

Mensurally, birds from Torrent are intermediate between *leucofrenatus* and *melanochloros*. Although only two males and a female overlap with *leucofrenatus*, the means for both sexes are significantly less (by more than 6 mm.) than means from northern Misiones samples, and only a single male and a single female from Torrent exceed the averages for Misiones. One Torrent specimen has a bill longer than its tarsi (a condition never found in *melanochloros*). The means for bill length are intermediate (both sexes), with specimens exceeding the bill length of *melanochloros* (12 of 31 specimens) and falling short of that in *leucofrenatus* (17 specimens). Since *melanochloros* barely has shorter tarsi than those in *leucofrenatus*, it is difficult to show intermediacy. However, the means for the Torrent sample exceed the means of *melanochloros*, falling within the range of *leucofrenatus* means, and seven males and three females exceed the range of *melanochloros* in tarsal length. Finally, in tail/wing ratios the Torrent birds bridge the nonoverlap area between the two forms. The means are intermediate, but tending slightly toward the means in *leucofrenatus* (both sexes). Of 30 birds, 25 fall in the intermediate range, outside the ranges of seasonally comparable samples of both *melanochloros* (northern Misiones) and *leucofrenatus* (Entre Ríos); four of the other specimens overlap with *leucofrenatus* and only one overlaps with *melanochloros*.

In wing length the Torrent specimens, like those from Colonia Garabí, Cuay Grande, and Alvear exceed wing length in both *leucofrenatus* and *melanochloros*. The mean difference (of 4 to 5 mm.) is highly significant for the male sample (significantly greater than both northern Misiones and Entre Ríos birds, in each case with $P=0.99$ according to Student's T test analysis),

and the females are significantly longer-winged than Entre Ríos birds, but not Misiones specimens. Since shorter-winged populations occur to the east (Rio Grande do Sul) and west (south-central Corrientes), as well as to the north and south, the long-winged tendency of these intermediates is noteworthy, and may be attributable to heterosis.

ALVEAR

The small sample ($N=5$) from Alvear is similar to the Torrent sample, but tends more toward *leucofrenatus* in some features of the specimens. Hence this sample comes from very near the center of the zone of hybridization between *leucofrenatus* and *melanochloros*. Four of the five specimens lack even traces of olive color in the ear coverts (only three of 17 Torrent birds do so). One of the Alvear specimens has a very broadly black area behind the malar (none of the 31 Torrent specimens so tends toward *leucofrenatus*). Four of five Alvear birds are intermediate or tend strongly toward *leucofrenatus*, compared with eight of 31 Torrent flickers. The mean bill length of four females is within the range of *leucofrenatus*, not intermediate as is that of the Torrent sample, and the bill of one bird exceeds in length that of all specimens from Torrent. Too, the Alvear specimens tend to have longer tarsi, although they are long even for *leucofrenatus*. Two birds have tarsi exceeding in length those of Torrent specimens, and one (female, 31.2 mm.) exceeds all Entre Ríos and Buenos Aires specimens as well.

The long-winged tendency evident in other hybrid zone populations of this transect is evident in the Alvear sample, owing to the presence of one long-winged female (152 mm.) which exceeds in wing length all *melanochloros* and *leucofrenatus* specimens.

SUMMARY OF EASTERN CORRIENTES TRANSECT

The intermediacy of birds in the samples from this transect, the clearly clinal nature of the shifts, and the variability in expression of characters both in individuals and in the various samples (i.e., characters are variously intermediate, tending toward *leucofrenatus*, and tending toward *melanochloros*) indicate hybridization as the cause of the observed variation. The hybrid zone extends from the vicinity of Colonia Garabí south (past Torrent and Alvear) an un-

determined distance but perhaps to a point just north of Paso de los Libros, Corrientes. Thus, the zone approximates 120 miles in length. Its width is not great, and is variable—indeed various hybrid populations may be almost or entirely disjunct (depending upon the dispersal and post-breeding wandering of this species, and these are unknown), because of the elimination of large portions of riparian forest along the Uruguay River. Even at its greatest width, near Colonia Garabí, it cannot be more than 10 miles wide. Of course, isolated forest patches back from the river afford some additional habitat, and relatively disjunct populations may occur in such situations (the forest patches on estancias seem less subject to severe cutting or elimination than is the riparian woodland). The prognosis for this area of contact is not good—that is, contact between *melanochloros* and *leucofrenatus* probably will become more tenuous as habitat for these woodpeckers is eliminated. This perhaps will permit stabilization in some of the entirely disjunct populations, due to unencumbered local selection factors and also some genetic drift because some of them are small in size.

THE CENTRAL CORRIENTES TRANSECT

The region of central Corrientes, away from the rivers bordering it on the north, west, and east is a sparsely inhabited, low area (fig. 3) containing the vast, poorly drained Esteros del Iberá. To the west and southwest of this marshland are fringes of the chaco woodlands. To the southeast and east, and in higher portions of the Esteros del Iberá are pampas grasslands. To the north is slightly higher, better drained ground principally containing pampas grassland mixed with palm-savanna and chaco woodland westwardly. At the northeast is an extension of the Misiones highlands into Corrientes, mainly pampas-savanna grasslands. Within the Esteros del Iberá, and the surrounding areas are small to large, disjunct pockets of woodland (presumably composed of both chaco and subtropical moist forest floral elements, but not well known botanically). These "montes" afford habitat for isolated, small to large populations of *Colaptes melanochloros*. Furthermore, unlike most areas where forests are connected by riparian woodlands, the woodlands of this region have no such connections (there are few definite streams, the woodlands being restricted to patches of pre-

sumably favored terrain). Hence, dispersal of flickers must take place across open, treeless areas to the extent that it occurs.

Because the woodlands of this region are disjunct, and many are of small size it is not surprising that the Green-barred Flickers found in this region tend strongly toward *C. m. leucofrenatus*, the form inhabiting the woodland patches of the pampas region to the south of the Esteros del Iberá. The presumed ability of flickers of this race to cross open areas and to forage on the ground seems to favor them in the habitat provided in central Corrientes. Few specimens are available from this region. William Partridge and his associates obtained a series of seven specimens from Colonia Carlos Pellegrini in the east-central part of the region during December, 1962. The same collector secured a single bird from the "Montes de San Antonio" in that same month; this locality is at the northeast edge of the Esteros del Iberá, only 30 to 50 miles south of Ituzaingó, but completely isolated from woodlands along the Parana River at Ituzaingó by extensive completely treeless pampas and esteros. Despite its distance (about 50 miles) from Colonia Carlos Pellegrini, the specimen falls within the range of variation of specimens from that locality, and it is included with them. Partridge also collected a series of six birds from the Río Aguapey, near San Carlos in northeastern Corrientes (almost on the Misiones border). This locality is in the highlands, and woodlands there are isolated by pampas from forests along the rivers to the northwest (Parana River) and southeast (Uruguay River). Although situated near the southern edge of the upland subtropical forest, it is somewhat disjunct from it, and seems to be inhabited by a flicker population that receives gene flow from the southwest, that is, from central Corrientes. The 14 specimens from these two (actually three) localities comprise the birds to be considered within the central Corrientes transect. Comparisons with them are made from: (1) samples of *melanochloros* from northern Misiones (N=65) and southern Misiones (N=11); (2) samples of *leucofrenatus* from Entre Ríos (N=51) and from Buenos Aires (N=24); and (3) samples from southern and western Corrientes (N=12; these are from Concepción and Mercedes, in the fringes of the Chaco at the west and south edges of the Esteros del Iberá), and from northwestern Entre

Ríos (N=14; also including eastern edge of Santa Fe). The specimens included under (3), as noted above, are close to *leucofrenatus* but show influence of *nigroviridis*; as they are from the areas adjacent to the Esteros del Iberá, and in the appropriate direction (southwest) from Misiones (and hence *melanochloros*), they must comprise the basis for comparison with the samples under discussion.

SAN CARLOS

Tables 1-3, 7

The small sample from San Carlos, situated in proximity to large populations of *melanochloros* along the Parana River, the Uruguay River, and the central Misiones highlands, nevertheless shows marked departures from *melanochloros*, representing tendencies toward *leucofrenatus* (and to some extent *nigroviridis*). Indeed, this sample compares favorably with that of the hybrid population from Torrent, some distance to the south and on the Uruguay River (see eastern Corrientes transect). Hence, overall, San Carlos birds tend to be more nearly intermediate between *melanochloros* and *leucofrenatus* than nearer the former race.

In color of the back five of six specimens tend away from the green typical of *melanochloros*, and three intermediate birds exceed variation in that form. Four of six specimens have the rump lighter in color than the back, whereas half to two-thirds of *melanochloros* specimens have these areas concolored. Although *melanochloros* and *leucofrenatus* do not differ greatly in tail barring, the latter tends to be less barred; barring tends to be less than normal for *melanochloros* in the San Carlos sample, and one female exceeds variation in *melanochloros* by having but a single bar on its inner vane of the outer (fifth) rectrix. The remiges lack dark pigment in four specimens, one shows traces of it, and only one shows a moderate (not full) amount of pigment, thus tending strongly toward *leucofrenatus* (a tendency in this direction is evident in the southern Misiones sample). Only one of six birds has the fully olive ear coverts found in the great majority of *melanochloros* specimens, whereas four specimens are intermediate to *leucofrenatus*-like (two birds lack even olive traces). Four specimens have blacker streaks behind the malar stripe than do the majority of *melanochloros* specimens, although the

range of variation does not exceed that found in *melanochloros*. In throat-breast color, five birds show moderate to strong orange-gold on the breast; all these exceed the variation found in *melanochloros*, and strongly tend toward *leucofrenatus*. Although four of six specimens have the fully greenish underparts of *melanochloros*, one bird is white below, and another is intermediate; both of the last two birds, of course, exceed the variation in *melanochloros*.

In mensural characters the San Carlos specimens are like both forms in wing length (no difference between *melanochloros* and *leucofrenatus*), and tend toward *melanochloros* in bill length (although one female has a bill length of 25.7 mm., exceeding *melanochloros* and equaling *leucofrenatus*), but they are intermediate or tend toward *leucofrenatus* in tail length, tarsal length, and tail/wing ratio. The four males exceed *leucofrenatus* and fall within the range of *melanochloros*, although not one is very long-tailed and their mean is 6 mm. less than that of comparably plumaged *melanochloros*. However, both females (tail length 98 and 99 mm.) are shorter-tailed than *melanochloros*—they exceed *leucofrenatus*, and hence fall in the intermediate (nonoverlap) area. The average tarsal length (males) exceeds that of *melanochloros*, and falls within the range of means of *leucofrenatus*. Four of six birds have tarsi longer than those of northern Misiones *melanochloros*, and one female exceeds southern Misiones specimens as well. Thus tarsal length of San Carlos birds tends toward *leucofrenatus*. Tail/wing ratios of males range from 0.70 to 0.72, below the range for seasonally comparably plumaged Misiones birds, but within the overall range of *melanochloros*. The two females, however, show ratios of 0.67 and 0.68, in the intermediate range and overlapping the range of *leucofrenatus*.

The San Carlos specimens are hybrids tending more toward *melanochloros* than toward *leucofrenatus*. They rather closely match birds from Torrent (or Alvear in color of remiges), but are perhaps slightly less intermediate (bill length as Colonia Garabí birds, tail and tail/wing ratios more like Cuay Grande birds). Thus, the hybrid zone extends into Misiones some distance (perhaps 20 miles) along the highland ridge between the Uruguay and Parana rivers, in contrast to the situations along those rivers. The tendencies toward *leucofrenatus* of the southern Misiones sample (reduced dark pigment in remiges, ear covert color, generally greater measurements)

probably are attributable to the proximity of birds of that sample to the hybrid zone.

ESTEROS DEL IBERÁ

Tables 1-7

Specimens from the Esteros del Iberá region rather strongly resemble *C. m. leucofrenatus*, for the reasons mentioned above. In the color of the back five specimens are *leucofrenatus*-like, whereas the other three are greener, one being intermediate (hence overlapping with the San Carlos birds); although not exceeding *leucofrenatus* samples in this trait, these specimens show more green than is found in the southern Corrientes-northwestern Entre Ríos samples. Only one bird has the rump as white as is typical in *leucofrenatus*; the green color in the whitish rumps of the others represents a trend toward *melanochloros*. In tail barring the Esteros del Iberá birds are like *leucofrenatus*. Dark pigment in the shafts of the remiges of half the specimens represents a tendency toward *melanochloros*; indeed more of these birds show pigment than do the San Carlos birds. The bird having the most dark pigment (hence overlapping with *melanochloros*) is from Colonia Carlos Pellegrini, not from the northeastern locality (Montes de San Antonio), although the single bird from the latter locality shows traces of pigmentation in its primaries. There is no trace of dark color in the ear coverts of these specimens, in strong contrast to those from San Carlos. Half the specimens have reduced orange-yellow on the throat, of course more than is normal for *leucofrenatus* (of 26 southern Corrientes-northwestern Entre Ríos specimens only two have such reduction). No intermediacy is shown in tail length, in bill length (all eight specimens have bills longer than those of *melanochloros*), in tail length, or in tail/wing ratio.

This sample and that from San Carlos show shallow, barlike breast spots; 13 of 14 birds have the spots wider than deep (93 per cent). This could be a chance occurrence, but *melanochloros* and *leucofrenatus* average 55 to 60 per cent and a value of 71 per cent (northwestern Entre Ríos) is the greatest otherwise attained in either race.

The Esteros del Iberá may be included within the hybrid zone, but are at its western edge.

SUMMARY OF CENTRAL CORRIENTES TRANSECT

Hybrid populations tending rather more

toward *leucofrenatus* than *melanochloros* occupy the Esteros del Iberá in north-central Corrientes, away from the major rivers bounding that province. At the northeast end of these esteros a rapid shift toward *melanochloros* occurs, but in the highlands back from the major rivers *leucofrenatus* influence is found even within Misiones. The San Carlos population, near the Misiones border, tends toward *melanochloros* but it closely resembles the hybrid population at Torrent, farther south along the Uruguay River. The prevalence of open country, and the discontinuous distribution of usually small woodlands in the inland region from central to northeastern Corrientes probably explain the stronger influence of *leucofrenatus* there, compared with the area along the Uruguay River.

THE NORTHERN CORRIENTES TRANSECT

The Upper or Alta Parana River joins the Paraguay River to form the (Lower) Parana River at the northwestern corner of Corrientes. The "L"-shaped riparian area formed by the first-mentioned two rivers is the region (fig. 3) most crucial for the interaction of the *melanochloros* and *melanolaimus* groups of Green-barred Flickers. The "L" itself is (or was) a virtually unbroken expanse of forest habitat, suitable for forest-adapted flickers. Inside the L, to the north and east, that is, in southeastern Paraguay, a variable population of flickers most resembling *C. m. melanochloros*, but tending toward *nattereri*, inhabits the pantanal (palm savannas) and broken patches of subtropical forest. West of the upper leg of the L is pantanal offering limited, but occasionally continuous woodland connections with chaco woodland farther to the west. South of the lower leg of the L are pampas and esteros, with occasional forest patches occupied by flicker populations most nearly like *C. m. leucofrenatus* (see central Corrientes Transect). In addition to the forests along the rivers, the Upper Parana River has many small and even larger islands, which often are entirely cloaked with dense forest. The riparian forests are directly connected with subtropical moist forests in Misiones, so that continuous gene flow from *melanochloros* is permitted along the rivers. As the riparian forests are sufficiently extensive to support populations of flickers, it is not surprising that natural selection might favor *melanochloros* genes in these populations. At any rate

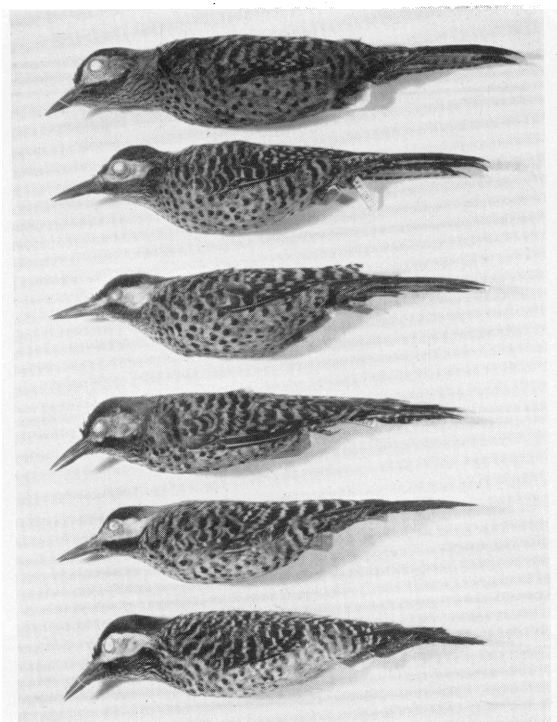


FIG. 4. Males of *Colaptes melanochloros melanochloros*, *C. m. nigroviridis*, and their hybrids. From top are: *C. m. melanochloros* (Misiones), four hybrids from vicinity of Ituzaingó (NE Corrientes), and at bottom, *C. m. nigroviridis* (NW Corrientes). Note shades of dorsal and ventral color, markings at rear of malar patch, ear covert color (dark versus white), bill length and tail length (see text).

these riparian populations tend toward *melanochloros* in appearance despite proximity to populations much more like the "*melanolaimus*" group to their west and south.

These generalizations aside, it is difficult to treat variation in the riparian populations. A major complicating factor is the occasional gene flow from the *melanochloros*-like Paraguayan populations (southeastern Paraguay) directly into the populations along the Upper Parana and the Paraguay rivers at diverse points. There is a cline apparent in samples taken from the Upper Parana River of northern Corrientes, but it is obscured by variability and by similarities between the western (Paraguay-Lower Parana River) populations generally representative of *C. m. nigroviridis* and the eastern populations which approach *melanochloros*. Thus, the situa-

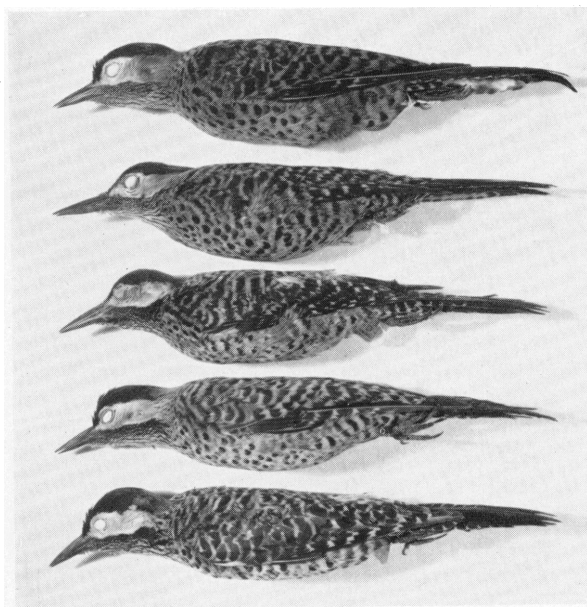


FIG. 5. Females of *Colaptes melanochloros melanochloros*, *C. m. nigroviridis* > *leucofrenatus*, and their hybrids. From top are: *C. m. melanochloros* (Misiones), hybrid from Ituzaingó (NE Corrientes), hybrid from 30 km. W Ituzaingó, hybrid from 25 km. E Ituzaingó, and, at bottom, *C. m. nigroviridis* > *leucofrenatus* (Mercedes, SW Corrientes). Note shades of dorsal and ventral color, markings at rear of malar patch, ear covert color (dark versus white), bill length and tail length (see text).

tion is less clear than that found along the Uruguay River.

Available from northern Corrientes are 41 specimens, representing localities (from east to west) around Ituzaingó, 30 to 40 km. west of Ituzaingó, just east of Itá-Ibaté, the Itatí-San Luís del Palmar region (fig. 3) of northwestern Corrientes, and an unknown locality in northern Corrientes, probably near Corrientes City. Comparison of these samples was made with specimens from Paraná-Santa Catarina (N=20), northern Misiones (N=65), and southern Misiones (N=11) representing *melanochloros*, and from eastern Chaco Province (N=9) and the southeastern corner of Formosa (N=11, including one Río Bermejo bird from northeastern Chaco).

ITUZAINGÓ

Tables 1-7

A sample of 12 birds was available from the

area within 25 km. east from Ituzaingó. These include: seven birds from the Estancia Puerto Valle, along the Upper Parana River 25 km. east of Ituzaingó, taken by William Partridge and his associates in November, 1962, and by me and R. S. Crossin in October, 1967; and three mainland birds and two specimens from an island in the same river, taken 14 km. north of Ituzaingó by Short and Crossin in October, 1967. In this region there are extensive although selectively cut forests bordering the river and dense forests containing much bamboo on the islands in the river. Cultivated land and pastures border the riparian forests, and no natural woodland occurs there or in the open pampas extending south from the riparian forest. There is no difference among specimens from the two localities, or between mainland and island specimens from north of Ituzaingó.

The specimens from this combined sample generally resemble *melanochloros*. They show definite tendencies toward *nigroviridis* (figs. 2, 4, 5) in most characters, however. In color of the back three specimens are quite brown above, exceeding *melanochloros*, and five other specimens are not fully green. This preponderance of off-green birds represents a tendency toward *nigroviridis*. Less than half of the specimens (five) have the rump colored like the back; such birds comprise more than two-thirds of the specimens in samples of *melanochloros*. The Ituzaingó sample shows less tail barring than *melanochloros*, with averages (e.g., central tail bars, bars on inner vane of outer rectrices) lower than those of *melanochloros* samples and falling within the range of *nigroviridis*. Two specimens lack dark pigment in the remiges, and four show only traces. None of the other six birds has the extensive dark pigment typical of *melanochloros*, and hence this represents a definite tendency toward *nigroviridis* (the southern Misiones sample of *melanochloros* exhibits a lesser tendency of this sort). More than half the specimens have reduced olive color in the ear coverts, and one almost has no indication of the pigment. Four specimens exceed variation of *melanochloros* in this feature. Only two flickers have the rear of the malar streaked like the throat as do two-thirds or more of the individuals in *melanochloros* samples; one male exceeds *melanochloros* in the great amount of black behind the malars, and six other specimens have moderately broad black streaks in that region. Three-quarters of the Ituzaingó

birds have traces to a moderate amount of orange-gold on the anterior breast, and four exceed the range of *melanochloros* in this trait, representing a distinct trend toward *nigroviridis*. Although *nigroviridis* shows an approach to *melanochloros* in color of underparts, the Ituzaingó birds are intermediate, constituting a sample matching no sample of either race. Two specimens attain the fully green underparts of *melanochloros*, exceeding variation in *nigroviridis*, but the others are paler and browner above (such off-colored birds comprise only 3 per cent of *melanochloros* samples). On the other hand, no specimen is as white below as are the great majority of *nigroviridis* specimens.

There tends to be considerable overlap in wing length between *melanochloros* and *nigroviridis*, but the latter averages longer wings. The females from Ituzaingó fall within the great overlap area, but tend more toward *melanochloros*. The more numerous males average greater wing length, exceeding the variation found in *melanochloros* samples, and one male with wings measuring 158 mm. exceeds *melanochloros* and is in the high range for *nigroviridis*. Two males and a female are shorter-tailed than any *melanochloros* specimen, and averages for both sexes are intermediate between *melanochloros* and *nigroviridis*, although tending toward the former more than the latter. Three males and two females exceed *melanochloros* in bill length, and means are intermediate (females) or tend more toward *nigroviridis* than toward *melanochloros*. One specimen has its bill as long as its tarsi, a state never found in *melanochloros*, and the mean difference between tarsal length and bill length (1.93 mm.) is near the range of means of *nigroviridis* rather than *melanochloros*. The tarsi of the two subspecies are so similar in length (one millimeter or so longer in *nigroviridis*) that intermediacy is not apparent in this feature. Weights are essentially similar in these two races also. Tail/wing ratios range from the low extreme of *melanochloros* (0.71 and 0.72) to the high range (0.67, 0.68) of *nigroviridis*. Five males have intermediate ratios (within the nonoverlap area between comparable samples of the two forms). Female ratios are intermediate (0.68, 0.70, 0.71, 0.71), although the ranges of the two forms barely overlap (at 0.70). Mean ratios are intermediate as well.

Overall, this sample comprises hybrids tending rather more toward *melanochloros* than

toward *nigroviridis*, but they are closer to being intermediate than being *melanochloros*.

ITÁ-IBATÉ

Tables 1-7

30 TO 40 KM. WEST OF ITUZAINGÓ

Figure 5

Three specimens were obtained by Short and Crossin in October, 1967, from an estancia situated 30 to 40 km. west-northwest of Ituzaingó, near the Upper Parana River. In this area the river flood plain is wide, and much of it has been cleared and devoted to cattle grazing and cultivation. However, woodland occurs along the ridge marking the outer extent of the flood plain, and this woodland extends short distances into the surrounding pampas wherever streams cut through the ridge from the south. Patchy forest occurs along the river, and islands in the river are heavily forested.

Although generally like the Ituzaingó specimens, these three flickers tend more toward *nigroviridis* in several ways. Two of the three specimens approach or attain back color typical of *nigroviridis* and these exceed variation in the Ituzaingó specimens. One bird lacks olive in the ear coverts, matching *nigroviridis*, and thus exceeding variation in Ituzaingó specimens; the other two flickers are intermediate or tend toward *nigroviridis* in color of ear coverts. These flickers tend more than Ituzaingó birds toward *nigroviridis* in throat color, one specimen exceeding the Ituzaingó variation in having a fully orange-gold patch on its throat and anterior breast. The specimens are nearer *nigroviridis* in color of underparts as well. One specimen falls within the low range of *nigroviridis* in tail length and in tail/wing ratio, exceeding variation in Ituzaingó specimens. In each character one of the other two birds is intermediate and the other falls within the range of *melanochloros*.

The center of the hybrid zone along the Upper Parana River probably lies in this region. Variation typical of hybrids is shown in the female specimen which has the very short tail and low tail/wing ratio. This bird also resembles *nigroviridis* in other measurements, in throat-breast color, and in the large amount of black to the rear of its malar patches. However, it tends more toward *melanochloros* than do both the other specimens in its intermediate back color, its somewhat green rump, in having a moderate amount of dark pigment in its remiges, and in its partly olive ear coverts.

This locality is situated about 53 km. west of Ituzaingó, and south of the river by about 1 km. The flood plain of the river is very wide here, and forest occurs in scattered patches (mixed with pastures and cultivated fields) in the flood plain, extensively on the islands, and continuously along the outer ridge of the flood plain. Collections were made at 3 km., 13 km., and 21 km. east-southeast of Itá Ibaté in late October and early November, 1967. The habitat was similar at all three sites except that forest was continuous along the river from 13 to 21 km. east-southeast of Itá-Ibaté, and for an undetermined distance eastward from there. Four specimens were obtained at 3 km. east, eight birds at 13 km. east, and three at 21 km. east of Itá-Ibaté.

The Itá-Ibaté sample contains hybrids tending to resemble *nigroviridis*. The area represented definitely lies west of the center of the hybrid zone. The color characters of birds in this sample are more *nigroviridis*-like than those of the Ituzaingó sample except for tail barring (both samples nearer *nigroviridis*) and the amount of black at the rear of the malar (both samples about the same, distinctly intermediate, tending neither toward *nigroviridis* nor *melanochloros*). In color of the back seven specimens are more *nigroviridis*-like than any specimens of the Ituzaingó sample (and falling within the range of some *nigroviridis* samples, e.g., that from southeastern Formosa). The rump color of Itá-Ibaté specimens tends rather more toward *melanochloros* than toward *nigroviridis*, but not so much as does that of Ituzaingó specimens (only three of 15 birds have the rump concolored with the back, versus five of 12 Ituzaingó birds, and one specimen from Itá-Ibaté is very white-rumped like the more white-rumped extreme specimens of *nigroviridis*). More than three-quarters of the Itá-Ibaté birds have no black pigment (six birds) or only traces (six birds) of such pigment in the remiges, whereas half the Ituzaingó flickers have a moderate amount of dark pigment, and only two specimens lack it. More than half the Itá-Ibaté specimens lack olive color in the ear coverts (only three have a moderate amount); no birds from Ituzaingó lack olive, and five of them exceed Itá-Ibaté specimens in attaining the full *melanochloros* condition. Most

Itá-Ibaté birds have a moderate to strong orange-gold throat-breast patch, but specimens exhibit the entire range from fully orange-gold to total lack of such color (in one specimen; the Ituzaingó birds lack it, and that sample tends distinctly toward *melanochloros*). Almost half the Itá-Ibaté specimens exceed variation in Ituzaingó birds by attaining the pale underparts typical of *nigroviridis*, and the sample tends toward *melanochloros* no farther than an intermediate condition (three of 15 birds; six Ituzaingó specimens are more like *melanochloros* than any Itá-Ibaté bird).

In mensural characters the Itá-Ibaté flickers differ little from Ituzaingó birds. In weight and wing length there is little or no difference between *melanochloros* and *nigroviridis*. In tail length both Itá-Ibaté and Ituzaingó flickers are intermediate, and in bill length they both tend toward *nigroviridis*. Both samples are nearer *nigroviridis* in tarsal length. However, in tail/wing ratio the Itá-Ibaté specimens tend away from the more intermediate Ituzaingó sample and toward *nigroviridis*. Five specimens are more *nigroviridis*-like than any Ituzaingó flicker. Only three specimens barely reach the low extreme (0.70, 0.71) of *melanochloros*. The Itá-Ibaté birds cannot be considered *nigroviridis* by this trait, because most are intermediate and their low extreme barely reaches the average ratio for *nigroviridis* (*nigroviridis* samples, and indeed samples from all races of the *melanolaimus* group vary little in mean tail/wing ratios).

NORTHWESTERN CORRIENTES

Tables 1-3, 5-7

Available specimens from this region include six birds from Estancia Tuyúti, along the Upper Parana River about 52 km. west of Itá-Ibaté and in the Department of Itatí, and six from San Luís del Palmar some 79 km. farther west. Additionally, a Boucard specimen labeled "Corrientes" in the Paris Natural History Museum probably can be included; it may have been collected near Corrientes City. In this region subtropical-chaco riparian forests border the river, and mixed palm savannas and chaco woodland patches occur away from the river, providing rich habitat for the flickers.

This sample is included with *nigroviridis* samples. It seems not to differ markedly from other, variable samples of that race from adja-

cent regions, although showing perhaps a greater tendency toward *melanochloros* in throat color, and in tail/wing ratio.

Although specimens from Tuyúti and San Luís del Palmar are generally similar, the more eastern Tuyúti sample tends more toward the Itá-Ibaté sample, and toward *melanochloros*. These tendencies involve especially: back color (two intermediate birds versus none for San Luís del Palmar); rump color (three of four birds tend more toward *melanochloros* than any of six from San Luís del Palmar); color of underparts (one intermediate bird, versus none from San Luís del Palmar); tail barring (mean number of central tail feather bars 6.67 versus 4.67, and bars on inner vane of outer rectrix 5.50 versus 3.00 bars in San Luís del Palmar birds); tail length (two Tuyúti birds at 102 and 104 mm. fall within the range of *melanochloros*; none of the San Luís del Palmar birds does so, and their lower extreme is less); and tail-wing ratio (mean 2 points higher, two specimens with intermediate range ratios versus none for San Luís del Palmar specimens). Considering all characters, four of six Tuyúti flickers probably are introgressant or hybrid birds, whereas only two of six San Luís del Palmar birds appear to be introgressants.

SUMMARY OF

NORTHERN CORRIENTES TRANSECT

Hybridization between *C. m. melanochloros* and *C. m. nigroviridis* occurs along the Upper Parana River of Corrientes (and undoubtedly of Paraguay on the north side of the river). The zone of hybridization extends probably from within the Misiones border just west of Posadas west to a point somewhere between Itatí and Itá-Ibaté (perhaps Tuyúti is the western extreme), a distance of about 190 km. or 115 miles, comparing favorably with the width of the zone along the Uruguay River (120 miles). The hybrid zone corresponds almost exactly to that area where forest is completely restricted to the vicinity of the Upper Parana River (chaco woodland and palm savanna occur west of Itá-Ibaté and the subtropical forest extends outward from the river bottomland in southwestern Misiones). Most characters shift rather abruptly within the hybrid zone, but populations west of the zone show more influence of *melanochloros* than do *leucofrenatus* populations south of the hybrid zone along the Uruguay River. This is primarily attributable to proximity of Paraguay-Parana

river populations to populations of the *melanochloros* group inhabiting the area east and north of those rivers in southeastern Paraguay, and presumably to gene flow from them. A secondary factor is the rather extensive, more or less continuous forest habitat available along the rivers, perhaps favoring genes of the forest flicker (*melanochloros*) group. The center of the hybrid zone is situated just west (30 to 50 km. west) of Ituzaingó.

THE PARAGUAY CONTACT

INTRODUCTION

Different problems concerning Paraguayan Green-barred Flickers have been alluded to in discussions of variation in both the *melanochloros* and *melanolaimus* groups, and in the section concerning hybridization along the northern Corrientes transect. Briefly, the large Paraguay River tends to separate populations of the two groups (fig. 3). Their relative isolation is enhanced by open areas of pantanal (palm savanna and savanna) bordering the Paraguay River (back from the usually forested riverbank). West of the pantanal is virtually unbroken chaco woodland, inhabited by *C. m. nigroviridis*. The Paraguay River and the pantanal probably incompletely but fairly effectively separate *nigroviridis* from populations of the *melanochloros* group, except as follows: in the north, where *nigroviridis* probably interbreeds with *C. m. nattereri* west of the Paraguay River, as *nattereri* occupies Santa Cruz (specimens from the northern Paraguayan chaco and from the southern part of Santa Cruz are totally lacking; this area is poorly known and almost uncollected for birds); and in the south where *nigroviridis* extends eastward across the Parana River into northwestern Corrientes, and undoubtedly into Paraguay north of the Upper Parana and probably also along the east bank of the Para-

guay River for some distance north of its confluence with the Upper Parana, that is, in the southwestern corner of eastern Paraguay.

Complications arise in eastern Paraguay because of the intergradation of the more *nigroviridis*-like *nattereri* with *C. m. melanochloros* over much of that region. Contact of this eastern mixed population of the *melanochloros* group with *nigroviridis* probably occurs through sporadic dispersal of both across the Paraguay River, through meeting along the east bank of the Paraguay River in southernmost (eastern) Paraguay, and through their meeting along the Upper Parana River as discussed in the section on the northern Corrientes transect. Gene flow between the two groups is impeded by the efficacy of the river barrier, by isolation through distance, and by the extensive forest areas of east-central and northeastern Paraguay. These factors seem to favor strongly the genes of the forest-dwelling *melanochloros*.

A final complication is the supposed occurrence of a *melanochloros*-like ("*cristatus*") population far out in the Paraguayan chaco along the Río Negro, well within the range of *nigroviridis* (see discussion by Traylor, 1951, pp. 425-426). For reasons discussed below I consider the sample of Green-barred Flickers from "Riacho Negro" to have been labeled mistakenly. The birds involved represent the population in eastern (even far eastern) Paraguay, where they most likely were collected.

Available from Paraguay were 28 adult and two immature specimens representing about 11 localities in the (western) Paraguayan chaco, and 57 adult and one immature specimens from about 19 localities in eastern Paraguay. Represented, although by inadequate series, are most parts of eastern Paraguay (except the critical southwestern corner), and parts of the southern, central, and western Paraguayan chaco—but not the critical northern portion. Perhaps the most critical gap in material available is the almost complete lack of specimens from the borders of the Paraguay River (fig. 3). Except for two specimens labeled "Puerto Casado," a specimen from Lambaré just below Asunción, a single bird from Clorinda, just west of the river in Formosa, and a series from along the western edge of the river in Formosa south of Formosa City, material in the Paraguay region represents localities 25 km. or more east, or west of the Paraguay River. Until adequate material is

forthcoming from sites along the river, especially from points opposite each other, it will remain difficult to assess the degree of interbreeding between populations east and west of the river.

UPPER PARANA RIVER REGION, SOUTHEASTERN PARAGUAY

Tables 1-3

Three specimens from the Encarnación region, opposite Posadas, Misiones, resemble *melanochloros* of southern Misiones. In their very green plumage, long tail, great tail/wing ratios (0.72 to 0.75), and extensive dark pigmentation in the remiges of all three birds, the sample shows no difference from *melanochloros*.

Thirteen specimens from two other localities on the Upper Parana River of Paraguay, namely Puerto Gibaja and Capitán Mesa, generally resemble *melanochloros* but show definite *nattereri*-like tendencies. These include shorter tails (average for six August to October males 102.67 mm.), the less than fully dark remiges (shafts) in more than half the specimens (all have dark pigment, however), and the paler underparts of several specimens.

NORTHEASTERN PARAGUAY

Tables 4-7

Northeastern Paraguay is represented by a series of nine adults (see fig. 2) from the Cerro Amambay, 40 km. west-southwest of Capitán Bado and about 200 km. east of Concepción, and by a single bird from "Molinasque" (I find on maps a "Molinas-que" northeast of Rosario, and a "Molino-cué" farther north, east of Puerto Sastre; the Molinasque specimen is much smaller and more *nattereri*-like than are Rosario area specimens, so presumably it comes from the northern locality or from elsewhere in northeastern Paraguay).

These specimens are intermediate between *C. m. melanochloros* and *C. m. nattereri* in coloration and in size. Overall they perhaps resemble *nattereri* more than *melanochloros*, for all have pale underparts and rumps, all but one show a considerable reduction of spotting on the abdomen, and all but one specimen have tail/wing ratios less than 0.70. These are the most *nattereri*-like birds I have seen from Paraguay, although specimens are lacking from the northern border region of eastern Paraguay. These

birds differ from *nattereri* in their greener backs, all but one bird have at least traces of dark pigment in the remiges, and in wing length, tail length, bill length, and tarsal length. They have measurements greater than all *nattereri* samples except that from eastern Bahia, but their relatively short tails and greener color distinguish them from that Bahia sample. The Molinasque specimen seems more like these Capitán Bado birds than like any other Paraguayan specimens.

INTERGRADATION OF *nattereri* AND *melanochloros* IN EAST-CENTRAL PARAGUAY

North-south variation is difficult to assess because of the small sample sizes and scattered localities represented. Specimens from the Villa Rica region (N=6 adults, 1 immature) generally resemble birds from Encarnación and Misiones, but they tend to show lesser tail measurements and tail/wing ratios. Farther north, from 25 km. east of Rosario four specimens resemble Villa Rica birds, but perhaps are slightly smaller and they definitely show less dark pigment in the primaries (nearly absent in one bird) and paler rumps. Birds from 37 to 45 km. east of the Paraguay River in the vicinity of Horqueta, some 120 km. north of Rosario, clearly tend toward *nattereri* in measurements (shorter wings, tails, tarsi, lesser tail/wing ratios, overlapping Rosario specimens only in the last character), although in coloration they are quite similar to Rosario flickers. Unfortunately, no specimens are available from the region north of Horqueta, where I presume *nattereri* influence is much greater. Nevertheless, a cline is apparent in mensural characters, and it suggests a northward shift toward *nattereri* in central eastern Paraguay. I have ignored samples from west of Villa Rica in this discussion because they tend toward *nigroviridis*. Indeed, some *nigroviridis* interference with the *nattereri-melanochloros* cline is suggested, as noted below.

THE EAST-WEST ASUNCIÓN TRANSECT

It was possible to examine specimens from an essentially east-west transect at the latitude of Asunción, although sample sizes are woefully small. Available are: the Espinillo, Formosa, sample (N=14), from about 94 km. northwest of Asunción; a single bird from Clorinda, Formosa, on the west bank of the Paraguay River across from Asunción; a bird from Lam-

baré, 8 km. south of Asunción (east bank of river); two flickers from Aregua, 28 km. east of Asunción; four specimens from Sapucay in the hills 86 km. east-southeast of Asunción; and a composite sample (N=6 adults, 1 immature) from Villa Rica, Itape, and near Caaguazú (110 km. east of Asunción) all averaging about 147 km. east-southeast of Asunción. These specimens provide a tentative means of evaluating a transect (about 240 km. long) from west to east, that is, from *nigroviridis* in the Chaco, across the Paraguay River and into populations of *melanochloros* > *nattereri* (see fig. 3).

A critical point for the comparisons of samples in this transect is that the extreme western (Espinillo) and eastern (Villa Rica) samples appear to show some effects of introgression, that is, the Espinillo sample tends toward *melanochloros* more than does the Paraguayan Chaco sample, and Villa Rica birds tend more toward *nigroviridis* than do birds from farther east (see discussion of introgression below). Thus, clear differences between Espinillo and Villa Rica specimens exist only in color of the back, color of the shafts of the remiges, throat-breast color, color of underparts, and tail/wing ratio. In all other features there is slight to moderate and even complete overlap. Of course, the samples are readily separable despite overlap in so many characters, because the overlap is generally small and all specimens tend in most characters toward the respective forms that these samples represent.

The single Clorinda, Formosa, male (NMM 27.1690) resembles the Espinillo specimens (hence representing *nigroviridis*) in its features, although it is extreme for that sample in tending toward *melanochloros* by having dark pigment traces on its remiges, a reduced yellow-gold throat patch, and moderately greenish underparts. A female specimen (SMMH 552608) from Formosa City, also situated on the west bank of the Paraguay River, but 105 km. south of Clorinda, is similar to the Clorinda flicker in underpart color, but overall tends slightly more toward *nigroviridis*. Both birds have the irregular broad ventral spots of *nigroviridis*, not the more evenly rounded spots of *melanochloros*. A single male specimen (SM 31857) from Lambaré, on the east bank of the Paraguay River only 11 km. southeast of Clorinda, is more *melanochloros*-like than the Clorinda specimen in having less black at the rear of the malar, less gold on the breast,

in its tail/wing ratio (0.70 versus 0.63 for the Clorinda bird), and in its shorter bill (24.5 mm. versus 25.8 mm.). In throat color, tail/wing ratio and bill length it exceeds the variation in Espinillo flickers and tends toward *melanochloros*. However, the Lambaré bird is more *nigroviridis*-like than is the Clorinda specimen in color of the back (typical of *nigroviridis*), in lacking dark pigment in its remiges, in having whiter underparts, and in having somewhat irregularly shaped ventral spots. It exceeds variation in Villa Rica birds, and tends toward *nigroviridis* in back color, lack of dark color in the remiges, in lacking olive in the ear coverts, in having some yellow in its throat-breast (intermediate), and in color of underparts. The condition of its throat-breast is outside the range of variation of Espinillo birds, and of birds from samples taken farther east (Aregua, Sapucay, Villa Rica). Thus, this specimen exceeds variation in *nigroviridis* in four features, it exceeds variation in *melanochloros* in two characters, and it is intermediate in one trait. Hence it may be considered intermediate between *nigroviridis* and *melanochloros*, although perhaps tending slightly more toward the latter in the totality of its features.

The specimens from a locality nearest Clorinda and Lambaré are two birds from Aregua, 28 km. east of Asunción (it is indeed unfortunate that no series is available from Asunción or the Paraguay River between Rosario and Formosa City). Superficially these specimens appear *melanochloros*-like, but paler, perhaps tending toward *nattereri*. In fact they represent *melanochloros* > *nattereri* intergrades introgressant toward *nigroviridis*. The assignment of introgression from *nigroviridis*, rather than intergradation from *nattereri* as the cause for what appear to be *nattereri*-like color traits in the Aregua specimens is based upon three facts: (1) these specimens tend toward the larger *nigroviridis*, not the smaller *nattereri* in mensural characters; (2) specimens from the Rosario region north of Asunción and in the direction of *nattereri* influence are less *nattereri*-like (or more *melanochloros*-like), not more *nattereri*-like as one would expect if gene flow from *nattereri* was the cause of these traits in Aregua (and Lambaré) birds; and (3) evidence of a strong east-west, rather than a strong north-south cline from Lambaré to Villa Rica indicates greater introgression from *nigroviridis* than from *nattereri*. The Aregua specimens (male UMMZ 111391, and female

UMMZ 111392) are: long-winged (150 mm., male) and relatively short-tailed (tail/wing ratios 0.65, 0.68), very long-billed (26.0 mm., 25.7 mm., male and female, respectively), lacking in (male) or having only traces of (female) dark pigment in the shafts of the remiges, and relatively weakly barred in the tail (female). The male exceeds in variation *melanochloros* specimens (both sexes) from farther east in bill length, lack of dark pigment in the remiges, and tail/wing ratio; in the first and second of these this male is more *nigroviridis*-like than is the Clorinda specimen. The female exceeds variation in all specimens of *melanochloros* from farther east in its long bill, its weakly barred tail, and in tail/wing ratio (matched by one Sapucay specimen); it is more *nigroviridis*-like than is the Lambaré male in these features. Both specimens have bills longer than their tarsi, whereas only one other bird (from Villa Rica) from all of eastern Paraguay has the bill longer than the tarsi. Nevertheless, the green upper parts, weakly streaked throat region, reduced (lacking or traces of) gold on the throat-breast, relatively green underparts, evenly rounded ventral spots, render them more like *melanochloros* than *nigroviridis*. Their features suggest they could represent a population somewhat similar to that of Ituzaingó in northern Corrientes.

Sapucay specimens are more *melanochloros*-like than are Aregua flickers. They do tend away from Villa Rica specimens and toward *nigroviridis* in several characters, namely: one female has the back off-green; another has a whitish rump; one specimen has but traces of dark pigment in the shafts of the remiges; there are traces of gold on the breast of one specimen; two of the four birds have paler underparts than even the Aregua flickers; and three specimens have tail/wing ratios below 0.70 (from 0.68 to 0.69). All of these tendencies involve variation exceeding that in Villa Rica flickers. Indeed, the Sapucay sample is intermediate between Villa Rica and Aregua-Lambaré samples.

The Villa Rica specimens are nearly identical with Misiones specimens of *melanochloros*. Tendencies toward *nigroviridis* may include the longer bills and tarsi of several specimens, and broader ventral spotting. Reduction of olive in the ear coverts (three of six birds), pale underparts of one specimen, and lower tail/wing ratios (five specimens all in the low range of Misiones birds, i.e., 0.70 to 0.74) may represent tenden-

cies toward *nigroviridis* or *nattereri* or both.

Thus, I assign specimens from the Villa Rica region to *C. m. melanochloros*, although they tend slightly toward *nigroviridis* and probably *nattereri*. Birds from Sapucay and Aregua are considered *melanochloros* tending definitely toward *nigroviridis* (*melanochloros* > *nigroviridis*). The Lambaré specimen is a hybrid, *melanochloros* × *nigroviridis*, whereas Formosa birds are considered *nigroviridis* tending somewhat toward *melanochloros*. Since *nigroviridis* presumably occurs in the southwestern corner of eastern Paraguay (i.e., along the Upper Parana River opposite Itatí and westward, and along the east bank of the Paraguay River south of Formosa City), further material should demonstrate the existence of a south-north hybrid zone between Asunción and Formosa City (perhaps to Pilar on the Paraguay side) along the east side of the Paraguay River, and a southwest-northeast hybrid zone extending from the junction of the Paraguay and Upper Parana rivers northeast perhaps to San Juan Bautista and San Ignacio.

PARAGUAYAN CHACO

Tables 1-7

Green-barred Flickers from the Chaco of western Paraguay come almost entirely from localities far to the west of the Paraguay River (fig. 3). Two Puerto Casado specimens are the only ones available from near that river. There is little variation in the Chaco specimens, although they represent a vast area from Villa Montes, Bolivia, nearly to the Paraguay River, and from General Díaz in the north to Formosa in the south. There is a slight trend toward larger size from north to south, evident from the fact that the longest winged birds are from more southern sites. There is, however, greater variation between the Paraguayan Chaco and birds from near the Paraguay River in Formosa.

The only bird from western Paraguay and Formosa with a fully dark (color as on back) rump is from Espinillo, Formosa. Four of 31 Paraguayan Chaco birds have traces of dark pigment in the remigial shafts, whereas two of 14 Espinillo area specimens and five of 11 southeastern Formosa specimens do so. Likewise, although the difference is not significant, more eastern Formosa birds have dark color in the ear coverts than do Paraguayan Chaco birds (eight of 24 versus five of 31 birds, respectively).

Eastern Formosa flickers show more reduction of the golden color of the throat-breast region than do Paraguayan Chaco birds. Indeed, more than half (13 of 25) of the eastern Formosan birds show such reduction; only a quarter (eight of 31) of the Paraguayan Chaco birds do so (the difference is significant at the $P=0.99$ level, by Chi-square analysis). There is also a tendency for shorter bills in eastern Formosan flickers (means of Paraguayan Chaco males varied from 27.03 to 27.23 mm., of Formosan males from 25.58 to 25.67 mm., of Paraguayan females from 26.14 to 26.28, and the mean for a single sample of Formosan females was 25.47 mm.). That this tendency is significant is shown also by the existence of clines in the proportion of birds in which the bill is longer than the tarsi (from 41 per cent of Paraguayan Chaco birds, to 23 per cent of Espinillo specimens, to 9 per cent of southeastern Formosan flickers), and in the mean difference between tarsal length and bill length (tarsus less bill means—+0.07, +0.61, and +1.24 mm., respectively for Paraguayan Chaco, Espinillo, and southeastern Formosa samples). It is significant that every one of these tendencies is in the direction of *C. m. melanochloros*, which interbreeds with *C. m. nigroviridis* in the southern Paraguay-Corrientes region. I believe that they reflect introgression from *melanochloros* into the riparian (Paraguay-Parana rivers) and pantanal *nigroviridis* populations (there is some gene flow beyond them into the Chaco populations).

The Puerto Casado specimens are important, because they represent a northern Paraguayan riparian population. Despite the paucity of specimens, there seems to be evident a tendency toward *nattereri* in the two available birds. The specimens are small; their wings measure 143 and 142 mm., the tail of one is 96 mm. (other, tail 84 mm., very worn), primary 10 measures 37 mm., and primary 9 measures 85 mm. These measurements are at or below (four cases) the extreme low measurements of *nigroviridis*. Their bills, at 24.9 and 25.5 mm. also are at the low extreme of *nigroviridis* from the Paraguayan Chaco. In coloration they are essentially like *nigroviridis*, although one of the two has traces of dark color in its primaries, both have only slightly broader black streaks on the malar rear than on the throat, and one has a reduced amount of gold on throat-breast. Ventral spotting is reduced and the spots are round (not transverse

as in typical *nigroviridis*). In the absence of comparative material from adjacent areas to the east and north, especially along the river, it is impossible to account for these tendencies.

A specimen from General Diaz (in the Paraguayan Chaco northwest of Puerto Guaraní, and the northernmost locality known for *nigroviridis*) is typical of Paraguayan Chaco specimens of *nigroviridis*, although having dark pigment in the remiges (one of only four such specimens from western Paraguay). Comparative material is sparse from critical areas to the north and east. The single specimen available from eastern Santa Cruz, Bolivia (Bolivian specimens largely are from western Santa Cruz), is a little large and it has a light golden wash on its breast, but it represents *nattereri*. The nearest Mato Grosso locality represented by specimens is São Francisco (east of the Paraguay River and at the same latitude as General Diaz); the one specimen from there is typical of the larger, southern Mato Grosso *nattereri*.

Thus, except for the suggestion of tendencies toward *nattereri* in the Puerto Casado birds, evidence is lacking for the occurrence of interbreeding between *nattereri* and *nigroviridis* (as is evidence for intergradation of *melanolaimus* and *nigroviridis* westwardly). I predict that future field work and collection of specimens will yield conclusive evidence for the interbreeding of *nigroviridis* and *nattereri*.

THE RIACHO NEGRO PROBLEM

Tables 5-7

Four specimens in the University of Michigan Museum of Zoology collection, obtained between July 31 and August 16, 1939 by Alberto Schulze and his associate G. Haack form the main basis for Traylor's (1951) separation of *C. melanochloros* and *C. melanolaimus* as distinct species. These four specimens have as a locality on their labels "Riacho Negro—235 ab. mouth" and "Riacho Negro, 235 k. w." The label data on these and many of Schulze's specimens are fully typewritten. Diverse problems are presented by these specimens, and by this locality, other than the fact that, except for these four specimens, all available evidence indicates that the *melanochloros* and *melanolaimus* groups interbreed where they come into contact.

The locality "Riacho Negro" presents certain problems. "Riacho" is the Spanish diminutive

of "Río," and, obviously, various creek-sized streams could be assigned such a name, some of which might never appear on maps. The only "Riacho Negro" that I have found on any map is a small tributary of the Paraguay River variously and erratically placed between the Pilcomayo and Confuso rivers at about latitude 25° S. and longitude 58° W. The Map of Hispanic America locates two such streams, one entering near the mouth of the Pilcomayo River, and the other a tributary of the Pilcomayo near its mouth; neither extends into the Chaco more than 60 km. west of Asunción, Paraguay. This (or these) stream is not that used as the "Riacho Negro" by Traylor (1951). Streams designated as the "Río Negro" occur in Paraguay as follows: a small stream east of Asunción near Caragatatay; a small tributary of the Tebicuary River in southeastern Paraguay; a small but major river entering the Paraguay River across from Concepción and extending west through marshes (part of river is missing on maps because of its uncertain course in this region) westward in the Chaco some 170 km., between the Río Verde and the Río Siete Puntas; and, a small river in the Chaco entering the Paraguay River across from Rosario (about lat. 24° 30' S., long. 57° 15' W.), extending only 80 km. into the Chaco on some maps; however, on other maps this Río Negro is shown including the upper portion of the Aguaray-guazu River, which meanders along an uncertain course to slightly over 200 km. west of the Paraguay River (about 140 km. west is the town of Río Negro). The last river is that considered the "Riacho Negro" by Traylor. Other "Río Negro" rivers occur in adjacent Bolivia and Argentina. I have been unable to contact Schulze, who may be deceased by now, and hence am not certain that this "Río Negro" is his "Riacho Negro," although no other stream is a likelier possibility.

If we assume that the Riacho Negro locality of Schulze is about 235 km. up the Río Negro that flows into the Paraguay River west of Rosario, we proceed to the major problem—were the four flickers actually collected at this assumed locality? I believe that certain available information concerning specimens Schulze collected, and the flicker specimens themselves cast serious doubt on his having obtained them at this locality.

Data from labels of specimens and the catalogues at the University of Michigan Museum

of Zoology give the following picture of localities worked by Schulze and his associates G. Haack and J. Unger during 1939. Haack was collecting out of Rosario, and from Puerto Casado, Paraguay, in January, February, and April. Specimens labeled as having been obtained by Schulze and Unger at 240 km. west of Puerto Casado are dated from June 4 to June 28. The Riacho Negro locality (235 km. above mouth) is represented by specimens labeled as obtained by Schulze and Haack between June 19 and September 7. From September 25 to October 25 specimens bearing "Schulze and Unger" come from Puerto Casado. There are several critical points, and some problems here: (1) where was Schulze between June 19 and June 28? (2) were the various collectors actually together according to the labels? (3) how far out from each locality were specimens collected, and were specimens from extraneous nearby and distant localities pooled with those from major localities? and (4) were specimens obtained between these major localities, either along the Paraguay River, or on side trips, *possibly to the east of the latter river* (see below)? I suggest that the specimens bear labels added at some time after collecting. This is based on their being typewritten, and on the fact that Schulze and Haack field numbers for Riacho Negro specimens follow consecutively the Schulze and Unger numbers for Puerto Casado specimens, even though the dates for these localities overlap (i.e., numbers for Puerto Casado specimens of Schulze and Unger range to number 7737 taken on June 28, whereas numbers for Schulze and Haack specimens from Riacho Negro commence with 7740 on 19 June; specimens numbered 7738 and 7739 are not in the Michigan collection). Because the specimens bear no other (field) labels, and the typewritten labels were added later, there was apparently the possibility of a mixup. Within the sequence of numbers assigned to Riacho Negro specimens there are numbers out of sequence by as much as nine days (e.g., no. 8507 follows no. 8344 for August 5, whereas numbers 8504–8506 and 8508–8509 were not assigned specimens until August 14). However and wherever the specimens were labeled, there seems to have been ample room for errors involving localities and dates of collection.

The four specimens of *C. melanochloros* were obtained between July 31 and August 16, 1939,

within a period of only 17 out of the 81 days represented by Riacho Negro labels. It is surprising that this short period (actually July 28 to August 16) includes records of four species found in eastern Paraguay but never reported in western Paraguay. These are: *Forpus passerinus* (*xanthopterygius*), July 28; *Notharchus macrorhynchus* (*swainsoni*), July 31; *Tachyphonus coronatus*, August 13; and two *Hemithraupis guira*, August 11. Additionally, three specimens of *Polystictus pectoralis*, a species known from western Paraguay from only one previous specimen (Steinbacher, 1962), were collected on August 10 and 13. Although it is possible that, of 300 specimens supposedly taken at Riacho Negro, these could represent new records, it seems as likely or more so that specimens from elsewhere, probably eastern Paraguay, were included in the "Riacho Negro" locality. Most of the other specimens could have been collected in western or in eastern Paraguay, although as few, such as *Campephilus robustus*, are known as Chaco species primarily or exclusively (interestingly, *C. robustus* and *C. melanoleucos* are both represented from "Riacho Negro"; this is the only record of both taken "precisely" at the same locality).

My skepticism about the Riacho Negro locality is reinforced by certain problems involving other localities, notably "Puerto Gibaja." This village is situated in Paraguay across the Upper Parana River from the mouth of the Iguazu River, which separates Brazil from Misiones, Argentina. The major collecting locality of William Partridge, namely "Arroyo-Uruguai," (fig. 3) represented by more than 20,000 specimens, is only a few miles downstream from Puerto Gibaja on the Misiones side of the Parana River. Schulze's specimens from Puerto Gibaja include two of the chaco form *Celeus flavescens kerri*, known from considerably farther west in Paraguay. Partridge's specimens from Uruguai include at least (there may be more; his collection is widely scattered) five specimens of *C. f. flavescens*, the subtropical forest form expected in this region, but no *C. f. kerri*; no *C. f. flavescens* was obtained by Schulze. More unusual is the case of *Dendrocolaptes picumnus* and *D. platyrostris*. Brodkorb (1941) described *Dendrocolaptes picumnus extimus*, a new race (actually not distinct from *D. p. pallescens*, personal observ.) of that species, based on six specimens from "Puerto Gibaja" taken by Schulze, who apparently obtained no specimens of *D. platyrostris* there. This

is peculiar for several reasons. *Dendrocolaptes picumnus* is totally unknown from eastern Paraguay, whereas *D. platyrostris* occurs throughout eastern Paraguay. Hence, as Brodkorb (1941, p. 1) admitted, Puerto Gibaja is "several hundred miles beyond the recorded range" of *picumnus*. Furthermore, Brodkorb has shown that *D. platyrostris* and not *D. picumnus* was obtained by Bertoni essentially at Puerto Gibaja in the last century. The great number of specimens (50 at the American Museum of Natural History alone) of *Dendrocolaptes* taken by Partridge at Uruguai includes only *platyrostris*, and not *picumnus*. Thus, I consider it unlikely that the Puerto Gibaja specimens of *picumnus* actually came from that locality. Whether they came from eastern Paraguay is a moot point, for *platyrostris* and *picumnus* are not known to be sympatric. Thus, there are serious questions about the validity of locality data on at least some of the specimens collected by Schulze and his associates.

The four Green-barred Flickers bearing "Riacho Negro" as a locality represent a population from somewhere in eastern Paraguay. They are nearer individuals of *melanochloros* than individuals of *nattereri*, but definitely tend toward the latter. Indeed, they resemble most closely the birds in the sample from Capitán Bado, being more *nattereri*-like than are specimens from east of Rosario. This is an important point, because, if an isolated colony of the *melanochloros* group occurred in the Chaco at the Riacho Negro locality, as maintained by Traylor (1951), one would expect birds of this population to resemble the flickers of the nearest population of that group to the east with which they should be in genetic contact. Compared with Rosario specimens, these from Riacho Negro have: shorter tarsi (no overlap, even of Riacho Negro males and Rosario females); perhaps shorter tails; lesser tail/wing ratios; less green backs; less dark pigment in shafts of the remiges (one lacks it entirely); and paler and less spotted underparts. From the comparably plumaged (August) Horqueta sample the Riacho Negro birds differ by: markedly larger size, as indicated by greater wing and tail measurements (bill and tarsi are only slightly greater in length); less green backs; whiter rumps; less dark pigmented remigial shafts; paler ear coverts; and especially less spotted, paler underparts. The Riacho Negro specimens are like those from Capitán Bado in

color, but have longer wings and tails.

Some of the *nattereri* tendencies in the Riacho Negro flickers could be explained on the basis of *nigroviridis*, rather than *nattereri* influence. However, the uniformity of the four Riacho Negro birds in throat color, their fine, rounded spots and very short bills (20.9 to 23.8 mm., mean 22.30 mm.), suggest that their variation away from *melanochloros* is due to influence from *nattereri*. Riacho Negro flickers do not match the Horqueta or Rosario specimens, being too large for the former and too pale for either (see other characters above). I would suggest that they represent a population inhabiting the hilly interior of eastern Paraguay between Horqueta, Rosario, and Capitán Bado, if it were not for the fact that we lack knowledge of the Paraguay River flicker populations. It is conceivable that the Green-barred Flicker population from the Paraguay River edge between Rosario and Concepción (or even north of the latter) will prove to be the source of the "Riacho Negro" specimens, thus showing both *nattereri* and *nigroviridis* influence. These could have been obtained readily by Schulze or one of his collectors, for example in traversing the distance from Unger's station in the Chaco west of Puerto Casado, or from the latter itself to the Riacho Negro camp of Haack (i.e., by water along the Paraguay River, and up the Río Negro).

Chaco specimens of *nigroviridis* are available from these localities (fig. 3) with distances shown from the supposed "Riacho Negro" locality of Schulze and Haack: Fortín Nueve, 120 km. SSE (type locality of *nigroviridis*); Espinillo, Formosa, 135 km. SSE; La Urbana, Formosa, 125 km. SSW; Río Siete Puntas, 70 km. NNE; Makthlawaiya on Río Verde, 70 km. NE; Lichtenau, 140 km. NW; and Escalante, 135 km. NW (distances from "Riacho Negro" to Rosario and Horqueta, collecting sites for *melanochloros*-like samples, are, respectively 220 km. SE, and 210 km. ENE). Adult specimens from these localities show no strong tendencies toward *melanochloros*, and hence no effects of interbreeding with populations of that group in their midst. (Juvenal and immature specimens of *C. m. nigroviridis*, *C. m. nattereri*, and *C. m. melanochloros* are much more similar to one another than are adults of these races, but "Riacho Negro" specimens are adults, and two immature birds from Río Siete Puntas and Makthlawaiya are *nigroviridis* by virtue of their long bills, the gold on their breasts

and their very heavily marked malar regions.)

In view of the uncertainty concerning the location of "Riacho Negro," the likelihood that some specimens labeled "Riacho Negro" came actually from elsewhere, the resemblance of the four Riacho Negro specimens of *C. melanochloros* to birds from eastern Paraguay, and finally the evidence for interbreeding of the *melanochloros* and *melanolaimus* groups wherever they meet, I cannot accept the Riacho Negro specimens as evidence of sympatry between *C. m. nigroviridis* and *C. m. melanochloros* > *nattereri* (= "*cristatus*"). Because of the resemblances of *nattereri* to *nigroviridis*, it is most unlikely that *melanochloros* populations tending toward *nattereri* would exist sympatrically with *nigroviridis*, whereas just to the southeast the less similar *melanochloros* and *nigroviridis* would interbreed, as they do. Pending further field work and collection of specimens in Paraguay, it seems appropriate to assign the Riacho Negro specimens to *melanochloros* > *nattereri*, with their locality uncertain but probably northeastern Paraguay.

SUMMARY

Eastern Paraguayan Green-barred Flickers largely represent a *melanochloros* > *nattereri* irregularly intergradient series of populations, with *melanochloros* influence strongest in the southeast and *nattereri* influence greatest in the north. Hybridization between these populations and *C. m. nigroviridis* occurs along the western portion of the Upper Parana River, and inland (east) from the Paraguay River in the southernmost portion of eastern Paraguay. The Paraguay River is somewhat of a barrier to interbreeding between *nigroviridis* and *melanochloros* > *nattereri*, especially in the north, although specimens are lacking from the banks of the river. Nevertheless, available eastern Paraguay specimens indicate gene flow from the Paraguay River and western Upper Parana River populations (*nigroviridis*) into populations in the Asunción-Sapucay region. Likewise, Formosan and Paraguayan Chaco specimens of *nigroviridis* suggest a cline due to *melanochloros* introgression from southeastern Paraguay. The evidence for interbreeding between *nigroviridis* and *nattereri* in northern Paraguay is largely suggestive, for only two specimens are available from within 20 km. or so of the Paraguay River, and series are sparse (essentially only one from Horqueta) from within 150 km. of that river. The specimen

gap exists not only in the east-west direction across the Paraguay River, but in a north-south direction along that river and west of it, whence come only single-specimen samples from three or four widely scattered localities. The supposed sympatry of populations of the *melanochloros* group and the *melanolaimus* group is based upon four specimens resembling flickers from northeastern Paraguay. It is doubtful that these specimens actually came from the site in the Paraguayan Chaco ascribed to them by Traylor (1951). Problems involving the exact location of the "Riacho Negro" locality, and particularly the matter of whether the specimen labels are correct, make it unwise to base taxonomic separation of *C. melanolaimus* from *C. melanochloros* on these four flickers. The positive evidence that individuals representing populations of these two groups interbreed wherever they are known to meet rather indicates that they are unlikely to prove to exist sympatrically elsewhere, including western Paraguay.

RIO GRANDE DO SUL AND URUGUAY

Tables 1-7

Available from Rio Grande do Sul were 14 male and 13 female specimens of the Green-barred Flicker. Unfortunately, this critical state is largely unrepresented by specimens, especially the crucial central third of it. As we have seen (above), Uruguay is occupied by a somewhat peculiar, *melanochloros*-tending population of *C. melanochloros leucofrenatus*, although all specimens tentatively are assignable to the latter. Accepting the fact that Uruguay specimens tend away from *leucofrenatus* in the direction of *melanochloros*, that sample will be used as one extreme for comparison with Rio Grande do Sul birds. For the other extreme we may use Misiones, Paraná, and Santa Catarina (only five specimens are available from the latter) samples.

Eighteen specimens come from northern and eastern Rio Grande do Sul (from Erebangó east and south to Taquara). These birds are mensurally not distinguishable from *melanochloros*. In plumage features they resemble *melanochloros*, but they deviate significantly in the direction of *leucofrenatus* in several respects. Four of 16 specimens are very pale-backed, exceeding variation among 91 specimens from Paraná, Santa Catarina, and Misiones. Nine of 16 birds have the rump slightly to strongly paler than the back, and two of these exceed the variation among 91 *melanochloros*. One bird lacks dark pigment on its remigial shafts (no *melanochloros* specimen does so), three have but traces, and only four have the fully pigmented shafts typical of *melanochloros*. Five of 16 specimens have no olive color in the ear coverts, exceeding variation in all 89 *melanochloros* (one other bird matches the only intermediate *melanochloros* specimen, which comes from southern Misiones). Four of 17 flickers are off the typical throat color condition of *melanochloros*, versus nine of 91 *melanochloros*; two have the full gold color of the *melanolaimus* groups and two are intermediate (no *melanochloros* specimen is intermediate, and only one probably aberrant bird has gold on the throat-breast). Finally three of 17 specimens exceed all specimens of *melanochloros* in color of underparts, and more than half (eight of 17) are off the typical *melanochloros* condition, whereas but three of 90 specimens of *melanochloros* deviate from that condition. These shifts in coloration from *melanochloros* are in the direction of the *melanolaimus* group, probably as a result of introgression, and under the influence too of environmental conditions in an ecotonal (pampas-subtropical forest) situation.

One specimen from the hills of northwestern Rio Grande do Sul (Wurtemberg) is very worn, it is missing rectrices and the bill is broken. It appears to be near *melanochloros* in its features.

The only specimen from central Rio Grande do Sul is a flicker from Camaguam, near the east coast and midway between the north and south borders of the state. It is intermediate between *leucofrenatus* and *melanochloros* in back color, throat-breast color, the streaking on its throat and neck, tail length (101 mm.), tail/wing ratio (0.69), and bill length (24.1 mm.). It is like *leucofrenatus* in lacking dark coloring on its remigial shafts, in lacking olive in its ear coverts, and in its pale, transversely spotted underparts.

This combination of characteristics places this specimen outside the range of variation of north-eastern Rio Grande do Sul birds, and it represents a trend toward *leucofrenatus*.

Five specimens represent localities (Candiota, Pelotas, west of São Laurenço, Bagé) in the southeastern corner of Rio Grande do Sul. These birds definitely resemble *leucofrenatus* more than they resemble *melanochloros*. However, they tend toward *melanochloros* more than do Uruguayan specimens in rump color (one bird with concolored back and rump), back color (intermediate to fully *melanochloros*-like), remigial shafts (moderate dark pigment in two birds, traces in two, and none in one specimen), throat color (one lacks indications of gold), and color of underparts (three specimens more green than Uruguayan birds). They also tend to have short bills (three under 22.0 mm.), long tails (101 to 108 mm., last exceeding Uruguayan birds), and greater tail/wing ratios (0.68 to 0.73, in intermediate range). The Pelotas birds from near the coast are particularly *melanochloros*-like, whereas the inland birds tend more toward *leucofrenatus*, and the bird from Arroyo la Mina, Bagé (on the Uruguayan border), is most *leucofrenatus*-like. Obviously series from several localities within the region are required to define adequately the hybrid zone. It is conceivable that the zone is irregular, that is, that it extends south farther along the coast than inland.

Two specimens recently obtained by William Belton in the southwestern tip of Rio Grande do Sul (southwestern corner of Uruguiana Department) are assignable to *C. m. leucofrenatus*. These flickers, from just south of the hybrid zone along the Uruguay River, have shorter tails and lesser

tail/wing ratios than have other specimens from Rio Grande do Sul. They also have less barred tails and blacker areas behind the malar stripes (they are more like Entre Ríos specimens of *leucofrenatus* than of Uruguay in this respect). Only in throat-breast color does one of the two flickers tend toward *melanochloros* more than any Uruguayan specimen; in all other respects, they fall within the range of Uruguayan and Entre Ríos specimens of *leucofrenatus*.

Uruguayan specimens are not typical of *C. m. leucofrenatus*, as has been noted. Although the sample from Uruguay is small, variation away from Buenos Aires and Entre Ríos specimens seems likely, and has been noted also by Traylor (1951). Table 8 indicates the tendencies toward *melanochloros* that are evident in Uruguayan birds, involving at least six color characters. Introgression is suggested as the likely cause of these tendencies because: (1) Green-barred Flickers seem to occur throughout Rio Grande do Sul; (2) interbreeding seems to occur between *C. m. melanochloros* and *C. m. leucofrenatus* in Rio Grande do Sul; (3) Uruguayan populations are rather isolated from gene flow from *leucofrenatus* populations to the west (they perhaps are more exposed to gene flow from *melanochloros* to the north); and (4) environmental factors appear to be similar in Entre Ríos, north-eastern Buenos Aires, and Uruguay, hence selection relating to these factors is apt to be similar also.

BOLIVIA

Tables 1-7

Specimens are lacking from the lower valleys of central Bolivia where the highland *C. melan-*

TABLE 8
COLOR FEATURES OF *C. m. melanochloros* IN SOME SAMPLES OF *C. m. leucofrenatus*^a

Character	Uruguay			Entre Ríos			Buenos Aires		
	N	Off Colored	%	N	Off Colored	%	N	Off Colored	%
Back color	13	8	61	47	9	19	23	7	30
Remiges	14	3	21	47	3	6	24	0	0
Ear coverts	14	2	14	46	6	13	22	0	0
Malar rear	14	6	43	47	8	17	24	0	0
Throat-breast	14	4	29	49	3	6	24	1	4
Underparts	14	6	43	45	7	16	21	4	19

^a "Off-colored" birds are those deviating from the typical condition in *leucofrenatus*; in these characters the deviation is in the direction of *melanochloros*.

ochloros melanolaimus might be expected to come in contact with the lowland *C. m. nattereri*. All specimens of the former are from areas above an elevation of 5000 feet in the northeast (nearest *nattereri*) to 3000 feet in the west (Ayopaya, Cochabamba). Specimens of *nattereri* are available from as far west as Buena Vista, Santa Cruz, at an elevation of 1600 feet. Localities for *melanolaimus* in westernmost Santa Cruz are at Comarapa and Trigal, more than 100 km. from Buena Vista, and at a higher elevation (5000 feet or more). There is no indication of interbreeding between *nattereri* and *melanolaimus*, although the latter shows some convergence toward the former in a few characters (approaches *nigroviridis* and hence tends toward *melanochloros* in having some green color dorsally and ventrally), possibly due to introgression. There may be an ecological barrier of unfavorable habitat, such as dense forest (both forms favor woodland edges, not forests) preventing their contact. It should be noted that a similar dearth of material precludes determination of intergradation between *melanolaimus* and the adjacent *nigroviridis* in the Bolivian-Paraguayan Chaco.

CONCLUSIONS

Green-barred Flickers occupy diverse habitats over a wide area in eastern and southern South America. This species comprises two major groups of populations, the *melanolaimus* group of drier woodland and woodland edges in the southwestern part of the Green-barred Flicker range, and the *melanochloros* group inhabiting generally wetter savannas, woodlands, and forests. These morphologically distinct groups are convergent in their features wherever their ranges meet, that is, they hybridize. Samples from populations in the zone of hybridization are variable, no two birds being alike, and in the center of the zone all birds phenotypically are hybrids over an area of about 50 km. The zone in which most birds are hybrids is from 100 km. to about 150 km. wide. As so often is the case, this Hybrid Zone (Short, 1969a) coincides with an environmental shift, namely from moist forest to pampas and dry chaco woodland. Such a radical shift can be expected to result in phenotypic and genetic step-clines in variable, conspecific populations extending across ecotonal areas, due to selective forces operating in the two adjacent environ-

ments. The narrow hybrid zones are influenced too by the patchy, limited occurrence of favorable habitat in the ecotonal areas.

No zone of hybridization is known as yet in northern Paraguay and Bolivia, although there are a few suggestions that interbreeding occurs there. Only a few specimens and no adequate series are available from that area. It is likely that the *melanochloros* and *melanolaimus* groups interbreed in that region, as they do to the south, because their populations are more alike phenotypically there than they are farther south.

Introgression is limited to areas near the hybrid zone in the south and east (e.g., northern Rio Grande do Sul, southern Misiones on the *melanochloros* side, and Uruguay, northern Entre Rios, and Corrientes on the other side), although apparently affecting the *melanolaimus* group more (e.g., all of Uruguay) than the *melanochloros* group. Of course detectable introgression, based on a few external morphological features, is apt to be considerably less than actual introgression. One reason for greater apparent introgression in the *melanolaimus* group is that local, woodland-inhabiting populations of the latter may benefit especially from gene flow from the forest-inhabiting *C. m. melanochloros*. At the same time terrestrial adaptation by the *melanolaimus* group may be hindered by introgression from *melanochloros* (as well as by competition from *C. campestris*).

Farther north there seems to be considerable introgression into the *melanolaimus* group, although the hybrid zone has yet to be defined. Virtually all of *C. m. nigroviridis* seems affected by introgression, with evidence of a cline toward the hybrid zone in the southeast (southwestern Paraguay, Corrientes). Of the *melanochloros* group *C. m. nattereri* seems convergent with the *melanolaimus* group (various aspects of color pattern, tail/wing ratio). This could be the result of introgression favored especially by the similarity of habitats of *nattereri* (savanna, caatinga) to those of races of the *melanolaimus* group. It is important to note the strong faunal connection (Short, ms) between the chaco and the savanna and caatinga regions of Brazil (e.g., *Nothura boraquira*, *Xolmis irupero*, and many others have either the same races or allied races in the caatinga and chaco regions), indicating that strong contact between them has obtained for some time. Of course it is conceivable that the apparent convergence of *nattereri* with the

melanolaimus group is due to parallel evolution in environmentally similar areas. In any case, their environmental similarity might favor introgression between them.

Although the evolution of the *melanochloros-punctigula-atricollis* complex is discussed more fully below, it is important to note resemblances among *C. punctigula*, *C. m. nattereri*, and the *melanolaimus* group of *C. melanochloros*. All of these have a tendency toward a pale rump, weak to strong "whitening" of the underparts, a strong tendency for yellow, gold, or red coloring on the breast, and a low tail/wing ratio. Reduced spotting below is also shown by *C. m. nattereri* and *C. punctigula*. All features except breast coloring and reduced spotting probably represent changes from the ancestral conditions. These changes may have been influenced at least partly by introgression among these forms, which occupy adjacent ranges. *Colaptes atricollis* and *C. m. melanochloros*, which occupy very different habitats, appear to have retained the ancestral conditions of these features (breast colored as underparts, rump colored as upperparts, tail long as in related species of *Picus*). At the present time interbreeding is limited, at least partly by physical barriers between *C. punctigula* and *C. m. nattereri* (which appear not to meet although contact is possible in northeastern Bolivia and in Mato Grosso), and between *nattereri* and the *melanolaimus* group. *Colaptes melanochloros nattereri* is rather more affected by interbreeding with *C. m. melanochloros*. Although specimens of the latter show relatively few effects of introgression from *nattereri* beyond the vast zone of intergradation, and no effects of introgression from the *melanolaimus* group beyond the areas immediately adjacent to the hybrid zone, cutting of the subtropical forests of southeastern Brazil and Misiones, Argentina, is creating a more open environment within the range of *melanochloros*, perhaps favoring greater introgression from these sources.

At the present time the *melanolaimus* and *melanochloros* groups are connected by intermediate populations. Each has access to the gene pool of the other. There is some evidence of introgression well beyond the hybrid zone in the *melanolaimus* group. On the basis of their free interbreeding I consider these groups conspecific. Typological reasons (they are largely distinct away from the hybrid zone), practical reasons (each group has subspecies, so one has

to cope with a hierarchy within the species), or genetic reasons (limited introgression) might be advanced for maintaining these groups as separate species. I consider these reasons of interest for discussion, and for genetic and evolutionary considerations, but they are irrelevant to the taxonomic issue of whether these groups are biological species. The test for the taxonomic status of these forms is their sympatry or lack of sympatry. They are not sympatric, but are genetically connected as well as being kept allopatric by the occurrence of a hybrid zone. I prefer to let species define themselves wherever possible, rather than resort to artificial criteria such as the amount of detectable introgression (how much? based on which, and on how many characters? from how great a zone of interbreeding?).

COLAPTES PITIUS (MOLINA)

The Chilean Flicker of forest edges and semi-wooded central and southern Chile and the Andean slopes of southern Argentina is not marked by bright colors, and indeed it is the brownest of the flickers. In size it is similar to the Campo Flicker, except for its bill which is considerably longer. Its major traits are: the reduction of malar stripes, which are lacking in females and reduced to a few flecks of black or black and red in males; the absence of a nuchal patch (as in *fernandinae*, *campestris*, *auratus* in part, and *rupicola* in part); a fully black-gray crown, tending to be like that of *auratus* (in part), *rupicola*, and *atricollis*; very broad dorsal and ventral bars (broader by far than other flickers); a completely unmarked white rump, as in *rupicola*, most *campestris*, and most *auratus*; and pale eyes like *rupicola* (all other flickers have dark eyes).

The breast barring tends to be concentrated, giving the effect of a patch. The ventral barring breaks on the abdomen, so that this area is often pure white at the body midline. Unlike most flickers, including those with spots, which often tend to barring posteriorly (e.g., *melanochloros*, *auratus*), the Chilean Flicker has narrower bars posteriorly and broader bars anteriorly. The buffy white throat gives way sharply to the barred breast, however, often with a scattering of small spots as occurs in *campestris*. Other traits are: the very little white barring of the tail, the regularly and fully barred upper tail coverts, and the very little yellow of the bases of rectrices.

Individual variation in the depth of the bars is considerable. Wear affects the more broadly barred birds causing reduction and even elimination of the distal pale interspaces, so that a few birds appear all brown above and on the breast. Some birds have dark central streaks on the shafts of crown feathers, such that a streaked appearance results reminiscent of the streaked crown of *C. fernandinae*. Several specimens showed some cinereous traces on the white underparts. I did not study the molts and juvenal plumage of this flicker. However, young birds have a pale barred, gray crown, unlike most other flickers, although young of *Colaptes auratus* and of *C. rupicola* sometimes show such barring.

Geographic variation in *pitiús* is not great. The birds from the Argentine side of the Andes tend to be as heavily barred if not more so than Chilean birds (*contra* Wetmore, 1926, p. 224), and they have somewhat shorter tails. Their tail/wing ratios average 0.68 to 0.73 compared with the 0.71 to 0.79 of Chilean specimens. Greater sample sizes of the Argentine populations probably would indicate some overlap in tail/wing ratios. Racial separation of the eastern populations (*cachinnans*) from the Chilean birds (*pitiús*) is questionable, and if *cachinnans* is allowed, it must stand as a very weakly defined subspecies based essentially upon relative tail length. The seven adult specimens of *cachinnans* at my disposal fall within the range of variation of *pitiús* in bill length and width, and they are no less barred below than are specimens of *pitiús*—in fact they may be more heavily marked ventrally on the average. The racial variation in other flickers exceeds that apparently existing between *pitiús* and *cachinnans*. Pending documentation of differences between these supposed races, I suppress *cachinnans*, making it a synonym of *pitiús*, which becomes monotypic.

COLAPTES RUPICOLA D'ORBIGNY

The Andean Flicker is another of the highly terrestrial flickers, indeed, it is the most terrestrial woodpecker. Occurring above the forests (to an altitude above 5000 m., personal observ.) in the open puna grasslands of the high Andes, this flicker ranges from northern Peru to northern Argentina. Three races have differentiated in various parts of these highlands, and one is so well marked that it was once considered a separate species. The major characters of this flicker are: a very long and variable bill; pale

underparts with markings (narrow bars or spot-bars) generally restricted to the center of the breast; yellow eye color; dull orange-yellow or greenish yellow legs; and strongly yellow shafts of the rectrices, with much yellow evident dorsally.

Somewhat like *pitiús* (also *auratus*, in part, and *atricollis*) the Andean Flicker has a blackish gray crown. Its rump is immaculate yellow-white or buffy white, and the rump patch is very extensive. The alternating black and brown or buff-brown back bars are relatively narrow and closely spaced. Some individuals have a narrow red nuchal patch (see below). This species attains the largest size (weights to 204 gm.) among the flickers, and it is the only species that nests exclusively in the ground. It is also the only flicker that does not subsist mainly on ants.

Individual variation is great within the Andean Flicker. Involved are not only the usual variation in dorsal barring and ventral barring, but also variation in the shape of the ventral markings, the barring of the tail, the presence and extent of the nuchal patch, and other features. One male (CM 94464) from La Paz, Bolivia, has its throat streaked rather than unmarked, and these streaks become spotlike, then merge with the bars on the breast, reminiscent of the green flickers (especially *melanochloros*). Many birds have the anterior breast bars very spotlike, a tendency noted in *campestris* as well. The gular region of the throat often has faint or darker gray streaks or occasionally is all gray, especially in the northern form (*cinereicapillus*). There is considerable variation in the amount of yellow in the dorsal shafts of the rectrices, and also in the general tone (yellow versus white-buff in southern populations) of the underparts, which is to some degree affected by fading. Fading seems to pale the yellow and cinereous colors, making them whiter and buffier, respectively. Variation of 8 to 10 or even 12 mm. in bill length occurs in samples from some areas, exceeding variation encountered in the other flickers (too, the exceptionally long bill of *rupicola* is subject to damage and resulting differential growth such that irregularly shaped or extra long, forceps-like bills result—one such bird has a bill measuring 71 mm., over 23 mm. longer than that of other individuals). Many birds have barring on the flanks and especially the posterior abdomen.

The sexes differ principally in the color of the malar stripe, which is gray in the female and gray overlain posteriorly with red in the male. Males tend more often than females to have a nuchal patch, and they tend to have it more fully developed in those populations in which the nuchal patch occurs, perhaps a genetic carry-over from a distant ancestor in which males had more red on the head than females (as modern *atricollis*, some species of *Piculus*). Size differences are not pronounced between the sexes. The greatest difference occurs in bill length; males exceed females by 3 to 7 per cent. Females have barely if any shorter tarsi and tails than males, and only slightly (3 mm. or so) shorter wings. The sexual difference seems greatest in the northern *cinereicapillus*.

Young birds in juvenal plumage often show more barring or larger bars or spots on the breast than adults from the same population (e.g., juveniles of *cinereicapillus* resemble adults of *puna*) and their dorsal bars are broader. They have the fluffier plumage of juvenal woodpeckers in general. Bars in the upper tail coverts are fewer and spaced wider apart in young birds. Some juveniles have dusky barring on the rear of the crown, reminiscent of the fuller barring found in juveniles of *pitiús*. Juvenal remiges have paler yellow shafts than those of adults. These appear to be replaced essentially in the post-juvenal molt. Young birds also have dark eyes (red-brown); it is not known when the eyes become paler.

The molts of this species appear compli-

TABLE 9
MEASUREMENTS (IN MILLIMETERS) OF MALE ANDEAN FLICKERS
COLLECTED IN SEPTEMBER TO FEBRUARY^a

Form	N	Mean $\pm$ SE	SD	CV	Range
WING LENGTH					
N <i>cinereicapillus</i>	7	170.00 $\pm$ 1.29	3.42	2.01	164–174
S <i>cinereicapillus</i>	5	170.20 $\pm$ 0.80	1.79	1.05	168–172
N <i>puna</i>	9	164.22 $\pm$ 1.26	3.77	2.29	159–170
S <i>puna</i>	5	163.40 $\pm$ 2.06	4.62	2.82	157–167
N <i>rupicola</i>	8	166.90 $\pm$ 1.38	3.91	2.34	160–172
S <i>rupicola</i>	8	166.40 $\pm$ 1.70	4.81	2.89	158–172
TAIL LENGTH					
N <i>cinereicapillus</i>	6	123.17 $\pm$ 1.78	4.36	3.54	115–127
S <i>cinereicapillus</i>	5	119.40 $\pm$ 1.54	3.44	2.88	114–122
N <i>puna</i>	8	110.88 $\pm$ 1.89	5.36	4.83	105–119
S <i>puna</i>	5	109.60 $\pm$ 2.66	5.94	5.42	101–115
N <i>rupicola</i>	6	105.80 $\pm$ 2.48	6.08	5.74	97–112
S <i>rupicola</i>	6	107.00 $\pm$ 2.00	4.90	4.58	100–112
BILL LENGTH					
N <i>cinereicapillus</i>	6	42.50 $\pm$ 1.50	3.67	8.63	37.0–47.1
S <i>cinereicapillus</i>	7	41.21 $\pm$ 0.84	2.23	5.41	36.7–44.1
N <i>puna</i>	9	40.84 $\pm$ 0.98	2.95	7.22	36.2–44.9
S <i>puna</i>	5	40.12 $\pm$ 0.96	2.15	5.36	37.9–42.5
N <i>rupicola</i>	6	35.22 $\pm$ 1.41	3.45	9.78	32.0–40.0
S <i>rupicola</i>	8	43.71 $\pm$ 0.99	2.80	6.42	40.0–48.9
TARSAL LENGTH					
N <i>cinereicapillus</i>	7	31.11 $\pm$ 0.47	1.25	4.02	29.6–32.7
S <i>cinereicapillus</i>	9	29.09 $\pm$ 0.43	1.29	4.44	27.1–31.2
N <i>puna</i>	10	28.83 $\pm$ 0.29	0.92	3.21	28.0–31.0
S <i>puna</i>	5	29.80 $\pm$ 0.47	1.06	3.54	28.0–30.6
N <i>rupicola</i>	9	29.73 $\pm$ 0.31	0.94	3.15	28.1–30.8
S <i>rupicola</i>	8	30.35 $\pm$ 0.31	0.88	2.91	29.0–31.0

^a Samples of *S cinereicapillus* taken June to November, and *N rupicola* taken November to April.

Symbols: N, sample size; SE, standard error of mean; SD, standard deviation; CV, coefficient of variability; N, northern; S, southern.

TABLE 10
MEASUREMENTS (IN MILLIMETERS) OF FEMALE ANDEAN FLICKERS
COLLECTED IN SEPTEMBER TO FEBRUARY^a

Form	N		Wing length Mean (range)	Tail length Mean (range)	Bill length Mean (range)	Tarsal length Mean (range)
	Min.	Max.				
N <i>cinereicapillus</i>	8-11		167.38(161-174)	120.29(114-128)	40.13(33.5-45.0)	30.31(29.4-32.0)
S <i>cinereicapillus</i>	6-8		162.83(159-169)	113.17(106-123)	37.28(35.6-39.3)	29.51(28.0-31.3)
N <i>puna</i>	9-11		163.22(159-170)	111.80(106-118)	38.00(35.8-41.0)	28.79(27.2-30.3)
S <i>puna</i>	6-14		163.83(160-170)	109.25(102-118)	37.78(34.5-43.5)	29.04(28.2-30.2)
N <i>rupicola</i>	4-5		163.40(160-165)	104.75(96-106)	38.10(33.8-40.7)	28.80(26.5-30.5)
S <i>rupicola</i>	8-8		163.00(156-170)	108.60(92-117)	37.32(32.8-41.5)	29.49(28.6-31.0)

^aSamples of *rupicola* include worn birds taken as late as March and April, although most specimens represent January and February. Tarsal length for *S. puna* is from April to September sample (tarsal length does not vary seasonally).

Symbols: N, sample size; min., minimum; max., maximum.

cated, and further material is needed before they can be understood. I have encountered specimens undergoing wing molt in every month except October and November. It seems possible that birds of higher elevations may have a somewhat different molt regimen than flickers from lower elevations. Most flickers undergo the annual molt from January until May or June. August birds from Cerro de Pasco and Junín were found to be completing their molt. It appears that the molt of the remiges may be protracted, perhaps correlated with the high altitude and considerable amount of flying accomplished by these wide-ranging birds.

GEOGRAPHIC VARIATION

The Andean Flicker exhibits some clinal north-south variation, and considerable discontinuous variation, also oriented from north to south. Three groups of populations have been designated as races, and these can be defined rather readily if not completely by the presence or absence of a red nuchal patch. The northern form, *cinereicapillus*, mainly lacks a nuchal patch; 91 per cent of the specimens show no traces and the others have it partly developed at best. The central race, *puna*, is characterized by a full red nuchal patch, which is present in more than 95 per cent of the flickers of this race, although it is reduced in extent in some females. The southern subspecies, *rupicola*, generally lacks a nuchal patch (88 per cent of specimens). Although there are other differences between the

central and southern populations, they are very similar and contrast as a group with the more divergent northern population.

A few other tendencies parallel discontinuous variation in nuchal pattern. The northernmost and southernmost samples tend to have greater tarsal length averages (tables 9 and 10) than do populations from the central region. Also, the outermost primary (P 10) averages 52 to 56 mm. in length in the southern, and 54 to 56 mm. in length in the northern samples, but only 47 to 52 mm. in the central samples. These differences may reflect a gap between *cinereicapillus* and the southern two groups of populations, combined with a north-south cline in the latter. However, there is apparently certain clinal variation including all three groups of populations, oriented from north to south. These clines involve tail barring, barring of the upper tail coverts, underpart color, ear covert color, ventral markings, and possibly tail length. In these features the extremes are found in the terminal populations, whereas central populations are intermediate.

In tail barring, *cinereicapillus* is the most variable, the bars being complete, incomplete, or even obsolete. More than half the specimens have irregular or obsolete barring. Bars reaching the rachis of the outer large rectrix on its inner vane average from 3.7 to 8.6. Tail barring is variable in *puna* as well; up to 20 per cent of the specimens have irregular barring. However, the number of bars is less than in other races, and the bars reaching the rachis from the inner vane

TABLE 11
SAMPLE MEANS FOR RATIOS AND CERTAIN MEASUREMENTS (IN MILLIMETERS)
OF ANDEAN FLICKERS^a

Form	N Min.-Max.	Tail/wing ratio	Primary 9	Back bar depth	Breast bar depth	Breast bar width
MALES						
N <i>cinereicapillus</i>	6-7	0.717	107.83	3.53	1.55	10.0+
S <i>cinereicapillus</i>	5-9	0.702	105.67	3.34	1.63	9.0+
N <i>puna</i>	8-10	0.674	104.90	3.60	2.10	6.07
S <i>puna</i>	5-14	0.670	106.80	3.42	2.34	6.24
N <i>rupicola</i>	6-9	0.638	111.56	3.60	2.88	5.52
S <i>rupicola</i>	6-8	0.645	111.00	3.96	2.56	6.00
FEMALES						
N <i>cinereicapillus</i>	8-11	0.717	105.44	3.75	1.40	10.0+
S <i>cinereicapillus</i>	6-8	0.697	106.88	3.84	1.63	9.0+
N <i>puna</i>	9-11	0.680	102.33	3.30	2.03	6.20
S <i>puna</i>	7-8	0.663	105.57	3.13	2.45	5.89
N <i>rupicola</i>	4-5	0.630	108.20	3.40	2.58	4.88
S <i>rupicola</i>	6-8	0.666	107.63	3.74	2.50	6.25

^a September to February samples for tail/wing ratio and primary 9, and average mean from various seasonal samples for other characters.

Symbols: N, sample size; N, northern; S, southern; min., minimum; max., maximum.

of the outer rectrix average 2.3 to 3.7. The southern race *rupicola* has more regular barring, and exhibits the greatest number of bars. Fewer than 5 per cent have irregular patterns, and bars reaching the rachis on the inner vane of the outer rectrix average 7.2 to 13.1.

There is clinal variation in color of underparts, although the cline is not a smooth one. Northern *cinereicapillus* is darkest below, colored with cinnamon washed with gold. *Colaptes rupicola puna* is distinctly paler, the underparts varying from buffy yellow to cinnamon buff. At the other extreme, southern *rupicola* has the palest underparts, varying from buffy yellow to whitish. There is overlap between *rupicola* and *puna*, but not between *puna* and *cinereicapillus* (very worn specimens of the latter may approach *puna*). Paralleling this variation, although showing considerably independent expression, is the color of the ear coverts. The ear covert colors of the different forms are like those of the underparts, except that no gold is present, i.e., from cinnamon in *cinereicapillus* through buff in *puna* to whitish in *rupicola*.

The ventral markings on the breast are very shallow and wide in *cinereicapillus*, and they ex-

tend fully across each feather. Thus, this form has a finely barred breast. In *puna* these marks are deeper, and narrower. They generally do not extend across the entire feather, and sometimes they are wedge-shaped or even spotlike. The markings of *rupicola* are the deepest and narrowest of all races. Many of the marks are wedge-shaped and some are spotlike. There is great individual variation in the southern two races, but no specimens have the breast so narrowly barred as to resemble *cinereicapillus*.

In tail length (tables 9, 10) *cinereicapillus* shows the greatest measurements (averages 113 to 123 mm.; three of four samples average over 119 mm.). Averages for *puna* are from 106 to 114 mm., whereas they vary from 104 to 109 mm. in *rupicola*. Additional material may show that *rupicola* is indeed shorter tailed than *puna*, but only a tendency toward this can be shown at present.

Thus, *puna* is intermediate between *rupicola* and *cinereicapillus* in these several features.

In addition to the nuchal character and to characters varying more or less clinally, described above, *cinereicapillus* differs from *rupicola* and *puna* in the following: weight (from *puna*);

gular color; pattern of upper tail coverts; wing length; bill length (?); and tail/wing ratio (table 11).

Few data are available for weights of these flickers. Two females from northern Peru weighed 174 and 183 gm., and a male, 204 gm. Weights of specimens near *puna*, but tending slightly to moderately toward *cinereicapillus* (see below) seem to weigh somewhat less (males average 179.2 and 174.9 gm., females 174.0 and 164.4 gm., in two samples). Data are not available for *rupicola*.

All individuals of *cinereicapillus* have black in the gular region, and 20 to 60 per cent of them have considerable black. Only 2 to 6 per cent of *rupicola* and *puna* have much black in that region; most show traces or lack black. The pattern of the upper tail coverts of *cinereicapillus* is variable; the coverts are barred, but the barring is incomplete. The number of bars on the central upper tail coverts averages 6.4 to 8.5 in several samples. The barring of these coverts in *rupicola* and *puna* is mainly complete (bars not obscured, wavy, or otherwise irregular), and an average of 11.7 to 13.1 bars per feather was noted in various samples of these two races.

In mensural characters *cinereicapillus* appears to have slightly longer wings (averages 163 to 170 mm., versus 163 to 167 mm. in *rupicola* and *puna*), a longer tail (see above), perhaps a longer bill, and greater tail/wing ratios (averages 0.697 to 0.717; *rupicola* and *puna* average 0.630 to 0.680). There is no appreciable difference in tarsal length, or in depth of back bars among these races.

Colaptes rupicola cinereicapillus Reichenbach,
1854

This race is characterized by lack of a nuchal patch, dark cinnamon-colored underparts and ear coverts, shallow but broad breast bars, and a relatively long tail. Compared with other races, it also tends to be larger in size (wing length, weight), it has irregularly barred rectrices and upper tail coverts, a more golden tone below, and yellower tail shafts, as well as more orange-yellow legs, its overall color above is darker, and its gular area invariably shows some or much black. Young birds in juvenal plumage generally resemble adults (see discussion above), but their breast markings are more like those of adults of the more southern races.

Southern populations of *cinereicapillus* have

been separated racially ("*stolzmanni*"), but comparison of birds from Ancash and southern Huánuco with more northern specimens fails to justify such a separation.

The southern sample shows lesser measurements (tables 9 to 11) in most cases, but the differences are minute except for length of the tail in which the difference approaches significance (male mean 3.77 mm. less, female mean 7.22 mm. less than northern *cinereicapillus*), although the samples are not strictly seasonally comparable. Certainly, there is no trenchant feature, nor group of features that allows separation of most individuals of the southern from those of the northern population. Also important is the fact that the apparent differences between northern and southern samples represent tendencies of the latter toward *puna*. These tendencies are: lesser wing length (females only); lesser tail length; shorter tarsi; lesser tail/wing ratio; deeper breast bars; narrower breast bars; slightly paler underparts and ear coverts; less black gular patch; and slightly more barred upper tail coverts. Although further material is needed, it is likely that some or even most of these tendencies are valid. Thus *cinereicapillus* to some extent converges upon *puna* in the area adjacent to the region of contact with the latter.

Fifteen adults of *cinereicapillus* were examined representing the southern populations (Huánuco, Ancash, the border of Ancash, Lima, and Huánuco; also two birds from southern Libertad). The northern samples of *cinereicapillus* include 32 adults from western Amazonas, western San Martín, eastern Piura, Cajamarca, eastern Lambayeque, and northern Libertad. Three immature flickers were available from Libertad.

Colaptes rupicola puna Cabanis, 1883

This subspecies is characterized by its well-developed nuchal patch, gold-buff underparts and ear coverts, moderately deep breast bars, and relatively few tail bars. It is intermediate between *cinereicapillus* and *rupicola* in ventral markings, the irregularity of the tail bars, barring of the upper tail coverts, and possibly tail length. It is somewhat darker above than *rupicola*, but except for that and the features mentioned above, *puna* resembles *rupicola* closely. Further studies are needed to establish whether *puna* is shorter winged and has shorter tarsi than *rupicola*.

Available for study were 39 adults from Junín,

TABLE 12
MEAN MEASUREMENTS (IN MILLIMETERS) OF CENTRAL PERUVIAN
Colaptes rupicola^a

	Weight ^b	Wing length	Tail length	Bill length	Tarsal length	Breast bar depth	Breast bar width	Tail/ wing ratio	P 10 length	N
MALES										
<i>S cinereicapillus</i>	?	170.20	119.40	41.21	29.09	1.63	9.00+	0.702	55.00	9
Yanahuanca	179.20	164.40	111.60	40.45	29.16	1.98	6.26	0.680	50.50	5
Cerro de Pasco	174.89	164.38	113.40	36.44	27.89	1.97	6.02	0.680	48.44	9
<i>N puna</i>	?	164.22	110.88	40.84	28.83	2.20	6.54	0.674	50.80	10
FEMALES										
<i>S cinereicapillus</i>	?	162.83	113.17	37.28	29.51	1.63	9.00+	0.697	56.25	8
Yanahuanca	174.00	164.50	107.00	40.27	28.56	1.98	6.40	0.653	47.00	4
Cerro de Pasco	164.43	163.00	108.75	36.51	27.43	2.07	5.94	0.658	51.43	7
<i>N puna</i>	?	163.22	111.80	38.00	28.79	2.10	6.04	0.680	47.56	11

^a Seasonally comparable adults. ^b In grams. See text for localities. Symbols: N, sample size; P 10, primary ten.

TABLE 13
COLOR OF UNDERPARTS IN PERUVIAN
Colaptes rupicola^a

Sample	N	Character p	State p-i	i	i-c	c
MALES						
<i>N cinereicapillus</i>	12	0	0	0	1	11
<i>S cinereicapillus</i>	8	0	0	2	2	4
Yanahuanca	5	1	1	3	0	0
Cerro de Pasco	9	4	4	1	0	0
<i>N puna</i>	19	14	4	1	0	0
<i>S puna</i>	18	12	6	0	0	0
FEMALES						
<i>N cinereicapillus</i>	15	0	0	0	1	14
<i>S cinereicapillus</i>	8	0	0	0	6	2
Yanahuanca	4	1	2	1	0	0
Cerro de Pasco	7	3	3	1	0	0
<i>N puna</i>	17	14	3	0	0	0
<i>S puna</i>	24	22	1	1	0	0

^a Adult specimens only.

Symbols: N, sample size; p, condition like *puna*; c, condition like *cinereicapillus*; i, intermediate; p-i, tending toward *puna*; i-c, tending toward *cinereicapillus*.

TABLE 14
COLOR OF EAR COVERTS IN PERUVIAN
Colaptes rupicola^a

Sample	N	Character p	State p-i	i	i-c	c
MALES						
<i>N cinereicapillus</i>	12	0	0	0	0	12
<i>S cinereicapillus</i>	8	0	0	2	2	4
Yanahuanca	5	0	3	1	1	0
Cerro de Pasco	9	4	3	1	1	0
<i>N puna</i>	19	10	5	4	0	0
<i>S puna</i>	18	14	0	4	0	0
FEMALES						
<i>N cinereicapillus</i>	15	0	0	0	0	15
<i>S cinereicapillus</i>	8	0	0	0	4	4
Yanahuanca	4	0	2	2	0	0
Cerro de Pasco	7	3	3	1	0	0
<i>N puna</i>	17	10	5	2	0	0
<i>S puna</i>	24	19	0	5	0	0

^a Adult specimens only.

Symbols: N, sample size; p, condition like *puna*; c, condition like *cinereicapillus*; i, intermediate; p-i, tending toward *puna*; i-c, tending toward *cinereicapillus*.

eastern Lima, and southern Cerro de Pasco ("northern *puna*"), and 43 adults from Cuzco, Huancavelica, Ayacucho, Apurimac, Arequipa, and Puno. Twenty-five adults collected by J. Morony and me in central and northern Cerro de Pasco are nearer *puna* than *cinereicapillus*; these are discussed below. Seven immature specimens also were examined.

Colaptes rupicola rupicola d'Orbigny, 1840

This subspecies is characterized by the absence of a nuchal patch (most birds), pale whitish to buffy yellow underparts and ear coverts, deep, irregularly shaped ventral markings, and a tail with numerous, well-developed bars. It is also paler above than *puna*, often appearing almost white and black barred. Its upper tail

coverts generally are fully barred. Possibly this form has a shorter tail, longer wings, and longer tarsi than those of *puna*, but this remains to be established. Like *puna*, and in contrast to *cinereicapillus*, *rupicola* has less yellow in the rectrices, little or no black in the gular region,

a shorter tail and a lesser tail/wing ratio. Despite the resemblance of *rupicola* to *cinereicapillus* in the absence of a nuchal patch, *rupicola* is considerably more like *puna* than *cinereicapillus* (see above). Sixteen adult specimens were examined from La Paz and Cochabamba, Bolivia, and from southernmost Puno, Peru ("northern *rupicola*" sample). The Peruvian bird, from Desaguadero on the Bolivian border west of Lake Titicaca, is generally nearer *rupicola* than *puna*. It has traces of a nuchal patch, however (the only female *rupicola* showing such traces), and it probably is intergradient toward *puna*. Specimens are needed from the region east and west (e.g., between Desaguadero from whence comes a specimen with nuchal traces, but generally nearer *rupicola*, and Puno, represented by a specimen with an intermediate nuchal, but nearer *puna* overall) of Lake Titicaca to determine the location and nature of the intergradation of *rupicola* and *puna*. Eighteen adults from Jujuy and Tucumán, Argentina, comprised the southern sample of *rupicola*. Four juvenile specimens of this race were seen.

TABLE 15
BLACK COLOR OF THE GULAR REGION IN
Colaptes rupicola^a

Sample	N	Absent	Traces	Over 5 per cent black	Mean per cent
MALES					
N <i>cinereicapillus</i>	11	0	1	10	54.0
S <i>cinereicapillus</i>	8	0	0	8	27.0
Yanahuanca	5	0	3	2	8.0
Cerro de Pasco	9	3	4	2	5.5
N <i>puna</i>	16	8	4	4	4.6
S <i>puna</i>	17	6	9	2	3.2
N <i>rupicola</i>	9	2	5	2	3.5
S <i>rupicola</i>	9	5	4	0	2.0
FEMALES					
N <i>cinereicapillus</i>	13	0	5	8	23.0
S <i>cinereicapillus</i>	8	1	3	4	17.0
Yanahuanca	4	2	0	2	7.0
Cerro de Pasco	7	2	3	2	7.0
N <i>puna</i>	17	4	8	5	8.0
S <i>puna</i>	24	5	11	8	6.0
N <i>rupicola</i>	6	4	2	0	2.0
S <i>rupicola</i>	6	3	3	0	2.0

^a Symbols: N, sample size.

HYBRIDIZATION BETWEEN *CINEREICAPILLUS* AND *PUNA*

Tables 12-16

In view of the differences between *cinereicapillus* and the southern races of *C. rupicola*, I attempted to ascertain the nature of the contact between *cinereicapillus* and *puna* in August, 1968.

TABLE 16
BARRING OF CENTRAL UPPER TAIL COVERTS IN *Colaptes rupicola*^a

Sample	Males				Females			
	N	Bars complete	Bars incomplete	Mean number of bars	N	Bars complete	Bars incomplete	Mean number of bars
<i>N cinereicapillus</i>	12	1	11	7.59	15	0	15	6.40
<i>S cinereicapillus</i>	8	2	6	8.50	8	1	7	6.43
Yanahuanca	5	0	5	9.00	4	0	4	9.75
Cerro de Pasco	9	2	7	10.33	7	3	4	10.00
<i>N puna</i>	18	11	7	13.10	18	9	9	12.46
<i>S puna</i>	16	12	4	13.10	23	14	9	11.70
<i>N rupicola</i>	8	7	1	12.00	5	3	2	12.00
<i>S rupicola</i>	9	6	3	12.56	6	4	2	13.00

^a Adults only.

Symbols: N, sample size.

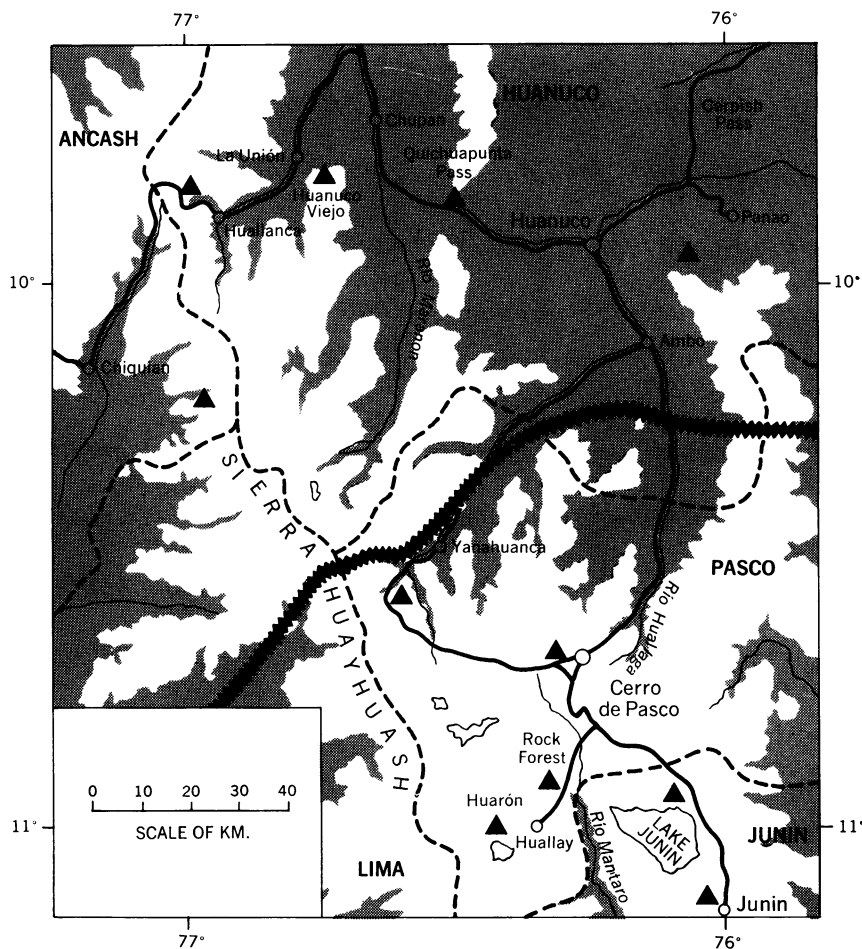


FIG. 6. Map of highland central Peru showing distribution of *Colaptes rupicola puna* and *C. r. cinereicapillus*. The solid black line with wavy edges crossing the map marks the approximate center of the area of interbreeding between *cinereicapillus* to the north, and *puna* to the south. Gray areas are at or below 4000 m. elevation. Triangles mark collecting stations (see text). Solid heavy black lines show major roads, fine black lines show major streams, and dashed lines show borders of the several departments. Modified from 1:1,000,000 map of Cerro de Pasco, Maps of Hispanic America, American Geographical Society, New York.

This attempt was only partly successful because of the terrain, the weather, and lack of roads. Individuals essentially like *cinereicapillus* were observed in several parts of southern Huánuco, namely: in the vicinity of Quichuapunta Pass (elevation 12,990 feet), at the headwaters of the Higuera River (fig. 6) northwest of the city of Huánuco, and in the vicinity of Hualanca and northwestward toward the Ancash border at elevations of 3500 to 4500 m. (fig. 7). Flickers resembling *puna* were seen about Lake

Junín, and north to Cerro de Pasco. Collections were made and birds studied in the field at sites between Cerro de Pasco and Yanahuanca, a village in the upper valley of the Yanahuanca River, a tributary of the Huallaga River which it joins near Ambo (see map, fig. 6). Specimens were collected primarily from 3 to 8 km. west of Cerro de Pasco at elevations of 4400 to 4600 m. (fig. 8), and in a small valley 15 km. southwest of Yanahuanca at 4050 to 4150 m., both along the Cerro de Pasco-Yanahuanca road. Flickers



FIG. 7. Puna NW Huallanca, western Huánuco, Peru, habitat of *Colaptes rupicola cinereicapillus*. Elevation about 4400 m. Note uneven aspect of terrain. Flickers probably nested in ravine along stream (center). Stone fences, rocks are used by them as perches.



FIG. 8. Puna habitat of *Colaptes rupicola puna*, introgressant slightly toward *cinereicapillus*, 8 km. W Cerro de Pasco. Elevation about 4500 m. Flickers perched and probably roosted in rocks, ranging out (to right) into grasslands for foraging.



FIG. 9. Small village in puna at 4000 m. elevation SW Yanahuanca, northern Cerro de Pasco, habitat of *Colaptes rupicola puna* $\times$ *cinereicapillus*. Flickers foraged down to this point from farther (right) up the valley, using stone fences as perches. Note cultivated fields (potatoes), old signs of cultivation, planted eucalyptus trees about houses.



FIG. 10. Puna habitat of *Colaptes rupicola puna* $\times$ *cinereicapillus* 15 km. SW Yanahuanca, northern Cerro de Pasco, elevation 4150 m. Flickers foraged in the lower grassy areas, retiring to the rocky slopes in time of danger. They nest and roost in holes in steep rocky slopes nearby.

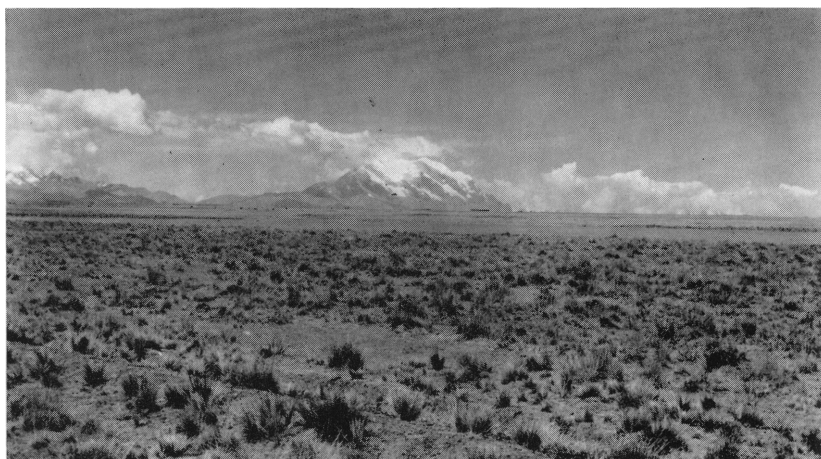


FIG. 11. Puna habitat of *Colaptes rupicola rupicola* on the Altiplano west of La Paz and south of Lake Titicaca, Bolivia, elevation about 3700 m. View looking toward eastern Andes Mountains. The grasslands show signs of recent burning. Flickers occur about villages and uneven places in the relatively flat terrain.

were seen at various points along the latter road, and there appears to be a continuous population of flickers in the region.

The area just discussed is precisely where the great Altiplano (fig. 11) extending across much of highland Bolivia and southern Peru terminates. Lake Junin is in the northern extreme of the Altiplano. North of that lake the landscape becomes hilly and irregular (vicinity of Cerro de Pasco). Still farther north, the highlands are greatly dissected and associated with abruptly rising mountains and deep valleys. Thus, *cinereicapillus* occurs in sharply dissected terrain at diverse altitudes, although generally above 3500 m. Its habitat is the steep slopes of small upland valleys. On the other hand, *puna* occupies the flat or gently sloping Altiplano, and the surrounding hills and valleys. Of course broken terrain occurs even in the Altiplano, and some areas adjacent to the Altiplano and occupied by flickers have very rough terrain. Nevertheless, there is no level plain of great extent occupied by *cinereicapillus*, and much of the population of *puna* inhabits flat or gently rolling country. It is likely that the nature of the interaction between *cinereicapillus* and *puna* is influenced by their adaptation to somewhat different habitats.

However, the major factor influencing the contact between *cinereicapillus* and *puna* is the deeply dissected highlands in the region of

northern Cerro de Pasco and southern Huánuco. Here the Marañón River, and particularly the Huallaga River have cut deep valleys from the north and east, and the Huaura River does the same on the west. These valleys (fig. 6) happen to cut into the towering Sierra Huayhuash, which attains elevations above 5500 and even 6000 m. The habitat suitable (i.e., areas above about 3700 m., and below 5000 m.) for these flickers thus is very much restricted. For example, the Huallaga and its tributary the Yanahuanca and the Huaura rivers have cut into the Sierra Huayhuash so much that the possible habitat for a north-south continuous population of flickers extends less than 20 km. from east to west, and elevations above 5000 m. and too-steep slopes within that area further restrict the distribution of flickers. The area of possible contact between *cinereicapillus* and *puna* may be narrower than 10 km. Of course, the flickers may sporadically cross valleys or otherwise circumnavigate physical barriers, but gene flow between the two forms nevertheless is very restricted.

The Yanahuanca and Cerro de Pasco samples from the area where contact might be expected between *cinereicapillus* and *puna*, were studied to establish whether there was evidence of interbreeding of these forms. Additionally, all available specimens from the region were examined

and compared with specimens from farther north and farther south. The northern *cinereicapillus* and southern *puna* samples served as reference (tables 12 to 16) points for consideration of possible interbreeding and of introgression into adjacent populations of these forms. Characters useful for such an analysis, as suggested from the material presented above concerning geographic variation are: nuchal patch, wing length, tail length, tail/wing ratio, depth and width of breast bars, color of underparts and of ear coverts, the amount of black in the gular region, pattern of the upper tail coverts, and perhaps tail barring. Comparisons were difficult because the samples were small and because the Yanahuanca and Cerro de Pasco specimens were collected while molting, and hence some of their features were obscured.

It is unfortunate that the Yanahuanca and Cerro de Pasco flickers were molting neck feathers, making it difficult to evaluate the nuchal patch in these birds. Only three of the 25 birds from these two localities appear to have fully developed nuchal patches; all three are from Cerro de Pasco. Three specimens from Yanahuanca and one from Cerro de Pasco show only a slight amount of red, and it is doubtful that these would have had a fully red nuchal patch following the molt. In fact, I estimate that no more than 12 of 16 Cerro de Pasco flickers, and no more than one Yanahuanca flicker would have had a completely formed nuchal patch following the molt. In this feature the Cerro de Pasco sample falls within the range of *puna*; the Yanahuanca sample appears intermediate between *puna* and *cinereicapillus*.

In color of underparts (table 13) the Cerro de Pasco flickers fall within the range of *puna*, although unlike *puna* a majority of the sample show deep buff and cinnamon traces. The Cerro de Pasco sample thus seems to tend somewhat toward *cinereicapillus*. Yanahuanca flickers do not exceed the variation in *puna* either, but they clearly tend toward *cinereicapillus*. If one considers the Yanahuanca flickers along with Cerro de Pasco birds as *puna*, then three of the five darkest *puna* males and one of the three darkest females come from Yanahuanca (one other male and one other female are from Cerro de Pasco). The preponderance of darker-bellied birds at Cerro de Pasco and especially Yanahuanca suggests interbreeding with *cinereicapillus*.

Even more suggestive of this are data for color of ear coverts (table 14). A majority of Cerro de Pasco birds are darker in this region than a majority of the birds in either sample of *puna*, and one specimen exceeds variation in *puna* in its approach to the cinnamon ear coverts of *cinereicapillus*. None of the Yanahuanca birds attains the typical condition of buff ear coverts for *puna*, or of cinnamon ear coverts of *cinereicapillus*. Rather, three specimens are intermediate, one is intermediate tending toward *cinereicapillus* and five are intermediate tending toward *puna*. One bird exceeds variation in *puna*, and five exceed variation in *cinereicapillus*, so the Yanahuanca sample tends somewhat more toward *puna* than toward *cinereicapillus*.

There is little evidence of hybridization from color of the gular region (table 15). Males of the Cerro de Pasco and Yanahuanca samples tend to have more black than those of samples of *puna*, and the Yanahuanca sample is the only *puna* sample in which all males show some black. Females of these two samples fall within the range of *puna*.

In the pattern of the upper tail coverts (table 16) Cerro de Pasco and Yanahuanca flickers are intermediate between the two forms. Intermediacy is shown particularly by the number of bars per feather, which is greater than in *cinereicapillus* and less than in *puna* (Yanahuanca birds tend more toward *cinereicapillus* than do Cerro de Pasco specimens). The flickers from Cerro de Pasco mainly (11 of 16 birds) have incomplete rather than complete bars, unlike other samples of *puna*. In this respect the Yanahuanca specimens are entirely typical of *cinereicapillus*, for all have incomplete bars.

No weights are available for *puna* and only a few (see above) data are available for *cinereicapillus*. The latter is apt to prove heavier than *puna*. Yanahuanca flickers are heavier than Cerro de Pasco specimens (both sexes; table 12) although the difference is not great. Wing length is not helpful in this instance because the southern *cinereicapillus* sample approaches *puna* (females). Male wing length means for Cerro de Pasco and Yanahuanca samples are like those of *puna*. Data for the length of primary 10 (table 12) in both sexes, for both samples, show overlap with *puna* also. The data for tail length are unclear, again partly because of the low range for females of the southern *cinereicapillus* sample. Males tend to be intermediate in this feature.

The molt stage of the birds in the two critical samples, especially the Yanahuanca sample, suggests that the central rectrices, the last to grow in, may not have attained their full length and hence the tail length may be unduly short in some specimens. Bill length is too variable, and tarsal length insufficiently variable to be useful in this analysis. Tail/wing ratios (table 12) are so similar in the northern *puna* and southern *cinereicapillus* samples that the data for this feature offer little for this analysis. Males may tend to be intermediate, whereas females show averages low even for *puna*, perhaps indicating molt effects (short tails possibly).

The breast bars of the Cerro de Pasco and Yanahuanca flickers seemed to me considerably variable but intermediate between *puna* and *cinereicapillus*. Comparisons show that only four specimens (three from Yanahuanca) from these localities exceed the great range of variation found in diverse (area, seasonal) samples of *puna*. These four birds have bars too shallow for *puna*, although none has the bars as wide as is found in *cinereicapillus*. Data for breast bar depth and width (table 12) indicate that the two samples are nearer *puna* than *cinereicapillus*, and that they tend somewhat toward *cinereicapillus* in the depth but not much, or any, in the width of the bars.

Overall the Cerro de Pasco sample resembles *puna*, but tends somewhat toward *cinereicapillus*. The Yanahuanca sample seems to represent a somewhat variable population intermediate between *puna* and *cinereicapillus*, but tending a bit more toward the former than the latter.

The data presented in various tables discussed above indicate not only intermediacy of Cerro de Pasco and Yanahuanca samples, but convergence of the southern *cinereicapillus* sample toward *puna*, and to a lesser extent, of the northern *puna* sample toward *cinereicapillus*. The southern *cinereicapillus* sample tends toward *puna* in:

- (1) wing length (females only).
- (2) tail length (both sexes).
- (3) possibly tarsal length (both sexes).
- (4) tail/wing ratio (both sexes).
- (5) breast bar depth (both sexes).
- (6) breast bar width (both sexes).
- (7) color of underparts (both sexes).
- (8) color of ear coverts (both sexes).
- (9) amount of black in the gular region (both sexes).
- (10) pattern of central upper tail coverts.

The northern *puna* sample tends toward *cinereicapillus* and away from southern *puna* in:

- (1) tail length (both sexes).
- (2) tail/wing ratio (both sexes).
- (3) breast bar depth (both sexes).
- (4) color of ear coverts (both sexes).
- (5) amount of black in gular region (both sexes).
- (6) irregularity of tail barring.

The convergence of these morphologically somewhat distinct but similar flickers approaching the area in which samples suggest their contact and interbreeding seems ascribable to introgression, although other factors may be involved and some of the tendencies suggested above may prove not to exist when more data are accumulated.

Available specimens from close to the area of contact, other than those discussed above (see also fig. 6), are several in number and they represent both forms. A female (AMNH 748546) from Jahuacocha at the border between Lima, Ancash, and Huánuco is small (wing 159, tail 106 mm., but worn), and its breast bars are not fully so wide as the feathers but otherwise it resembles *cinereicapillus*. Three adults from Huanuco Mountains east of Huánuco are generally like *cinereicapillus*, although one has deep breast bars and another has narrow breast bars. Possible hybridization with *puna* to the south is suggested by the fact that both males have partial nuchal patches, one showing only traces and the other a moderate amount of red. These specimens are of interest because the highland connection of the Huanuco Mountains is southerly toward Lake Junin (see fig. 6). The occurrence of *cinereicapillus*-like birds in these mountains suggests either colonization from the north or west across arid intervening valleys, or an earlier, more southerly occurrence of *cinereicapillus*. Three specimens from Huánuco Viejo, situated east of La Unión (fig. 6), are essentially like *cinereicapillus*, but the two males are very pale below and on the ear coverts, they are small (short wings, tails), and they have low tail/wing ratios (0.64, 0.65). These possibly represent tendencies toward *puna*.

The northernmost specimens of *puna*, other than those from Cerro de Pasco discussed above, are birds from the Rock Forest northwest of Lake Junin, from Huarón west of Lake Junin, from Paucartambo northeast of Lake Junin, and from "the Andes of Lima." Many other birds were

available from the immediate vicinity of Lake Junin, Junín, the Tarma region, and Oroya, all farther south. The Rock Forest specimen is *puna*-like in all respects. Three birds from Huarón seem to show tendencies toward *cinereicapillus*. These involve dark plumage (underparts, ear coverts of all three), rather narrow breast bars, and the apparent absence of a nuchal patch in one female. The Paucartambo specimen is long-tailed (118 mm.), but resembles *puna* in its features. The specimen from the Andes of Lima (BM 89.2.26.309) too has a long tail (119 mm., tail/wing ratio 0.72) but it is otherwise typical of *puna*. A sample of seven specimens from Maraynioc, northeast of Tarma is *puna*-like, but the birds tend to have narrow breast bars and long tails (tail/wing ratios 0.67 to 0.75, all but one over 0.70). This may reflect introgression from the Huanuco Mountain population of *cinereicapillus*.

CONCLUSIONS

The Andean Flicker is geographically variable with three discrete groups of populations. The southern two groups, *puna* and *rupicola*, are closely similar but show some differences in measurements and in color and pattern, particularly of the nuchal patch. The northern group of populations, *C. r. cinereicapillus*, is more divergent, exhibiting stronger color pattern differences, mensural differences, and some differences in proportion. Their variation is partly clinal and partly discontinuous, with shifts from one form to the other occurring over a small area. The areas of contact occur where barriers (Lake Titicaca for *rupicola*-*puna*, deep valleys for *puna*-*cinereicapillus*) appear to have isolated the populations more completely in the past; at present barriers permit very limited contact. In the case of both contact zones the forms involved exhibit character convergence. This convergence, involving a number of characters in the case of *puna* and *cinereicapillus*, and the variability of individuals representing populations situated near the zone of contact, indicate that hybridization and introgression are major factors affecting the evolution of this species.

Although no populations have been sampled that represent the center of a hybrid zone, the location of such zones can be hypothesized as the region east and west of the north-central portion of Lake Titicaca in the case of *puna* and

rupicola, and the region along the border of Huánuco and Cerro de Pasco in the case of *puna* and *cinereicapillus*. The narrowness of the contact zones seems due to extrinsic factors, namely physical (topographic, vegetational) barriers that greatly restrict gene flow. Not only is gene flow curtailed, but the operation of natural selection on this gene flow is permitted through the medium of a filter-barrier. Slight habitat differences between *puna* and *cinereicapillus* may enhance such selection in their region of interbreeding. The barriers may have been both more complete and less complete at times in the past, compared with the present situation. The convergence of *puna* and *cinereicapillus* near their zone of contact suggests either that selection is not operating to restrict greatly the flow of genes through the present narrow contact zone, or that there has been more gene flow and presumably broader contact in the recent past than occurs at present.

COLAPTES CAMPESTRIS (VIELLOT)

INTRODUCTION

The widespread, highly terrestrial Campo Flicker occurs in savannas and pampas, and in cultivated areas within as well as outside forests from Sipaliwini, Surinam (Mees, 1968), and Pará, Brazil, in the northeast and southern Beni, Bolivia, in the northwest south to Río Negro, Argentina (fig. 1). Within this vast area are two morphologically discrete groups of populations, a northern savanna and forest-clearing group, characterized by having a black throat, and a southern pampas and woodland-edge group lacking a black throat patch. These forms, often considered full species (*C. campestris* in the north, *C. campestroides* in the south), are largely geographically isolated by forest barriers. Both penetrate these barriers through nonforest corridors, which are becoming more frequent as the forests come increasingly under cultivation. The region of contact extends from central Paraguay (probably mainly along the Paraguay River and to the east of it), perhaps northern Misiones, and southern Santa Catarina. Evidence presented below indicates that the barriers to interbreeding between these two forms are extrinsic, that is, historically determined "accidents" of topography and vegetation, rather than intrinsic.

There is considerable individual variation,

especially in bill length, in the extent of barring on the rump and the underparts, and in the presence or absence of the malar stripes. The rump is usually white with a few bars, but a partly to fully barred condition is found in a few birds from all areas. The underparts are barred, usually heavily, but sometimes finely (especially in northern *campestris*). In three cases the breast bars are reduced, so as to appear more like spots than bars. These instances involve a female (BM 96.9.8.83) *campestroides* from the Pilcomayo River of Formosa, having bar-spots little wider than deep, a male (SM 552502) *campestris* from the Río Siete Puntas of western Paraguay with spots barely wider than deep, and a male from Bolivia (locality unknown, CM 33029) fully spotted below. Some individuals, especially of Bolivian *C. c. campestris*, are very yellowish below and a few even have green-yellow on the back. Noteworthy especially are a male (CM 328) and female (CM 50652) from Santa Cruz, Bolivia. The former has much pale green-yellow below and on the edges of many back feathers, and the latter bird also has some green-yellow on its back. The spotted bird (CM 33029) mentioned above also has much yellow below and yellow-green traces on its back. It shows no other tendencies toward *Colaptes melanochloros* (hybridization between *C. campestris* and *C. melanochloros* is unknown, but hybrids might occur very rarely), and these may represent effects of partial genetic reversion to an ancestral condition. The malar stripes of males vary in the amount of red and black (males), and of black (females). In some cases, especially in *campestroides* the malar may be very white, with only small flecks of black (females). In other cases, particularly in *campestris*, it is mainly black and red, or black, matching the black throat. The sexes differ in the malar color, males having red mixed with black, and females lacking red (at any distance the red is not visible to an observer). Differences in other features are trivial. Males perhaps have longer wings, and they tend to have a longer bill and longer tarsi than those of females, but the differences are of the order of 1 per cent. More female samples had tail length means greater than males, but the difference is so small that the sexes are virtually alike in tail length. Female samples tend to have slightly greater tail/wing ratios, so perhaps females do have slightly longer tails than males. Weights from 17 adults of

campestroides range from 151 gm. (a female) to 192 gm. (a male), but they are from diverse seasons; females may average slightly lighter than males. There is no sexual difference in barring (above or below) or in rump markings. The only other sexual difference is a tendency for females to have more white, less black throats (probably correlated with less black malars) than males. This means that more females than males of the black-throated *C. c. campestris* have white flecks on the throat, and more males than females of the white-throated *C. c. campestroides* show black flecks in the throat.

Juvenal Campo Flickers are colored very much like the adults; indeed, except for their more fluffy plumage, they appear like adults. As in *C. auratus* and *C. melanochloros* juveniles have paler yellow remiges than do adults, although the secondaries are rather darker (brown pigment present) dorsally than in adults. The outer primary is broader and longer than in adults. Juveniles tend to have blacker, less white-flecked malar stripes than adults.

Molt takes place between February and May, varying somewhat geographically. The annual molt is complete. Feather-wear effects are noticeable dorsally; the fine dark tips and the outer light interspaces gradually wear away, leaving the next dark bar prominent. The brown bars fade during the year. As a result, the birds appear brighter, with sharply defined dark and light bars in fresh plumage, and they become duller but browner with less distinct barring in worn plumage. Some severely worn birds appear almost completely brown above, because of the loss of white at the ends of the feathers. The feathers can become very soiled, especially in areas with reddish soils as in Misiones. The entire underparts, faces, and even the backs of some birds from these areas are rusty.

I scored throat color in a character scoring system, assigning 0 for the pure white of *campestroides*, and 4 for the all-black throat found in many *campestris*. Intermediate scores of 0+, 1, 1+, 2, 2+, 3, and 3+ were given for the graded series of intermediate scores, ranging from traces of black at 0+ to traces of white at 3+. The scores roughly indicate the per cent of black in the throat, i.e., 1 is 25 per cent, 2+ is 62.5 per cent, 3 is 75 per cent, etc. Individual variation is great, especially in *campestris* (see below). There is also a sexual difference, mentioned

TABLE 17
MEAN MEASUREMENTS (IN MILLIMETERS) OF WING, TAIL,
AND BILL LENGTH IN MALE CAMPO FLICKERS^a

Sample	Wing Length	Tail Length	Bill Length
September to December			
SE Brazil	162.75 (4)	—	27.68 (5)
Bolivia—M. Grosso	156.27 (11)	109.17 (14)	28.04 (15)
N Paraguay	157.00 (5)	105.80 (5)	27.68 (5)
NE Paraguay	159.83 (6)	107.83 (6)	27.78 (6)
Corrientes	160.60 (5)	108.60 (5)	28.16 (5)
Misiones	160.89 (18)	108.25 (16)	26.84 (18)
R. G. do Sul	162.86 (7)	110.57 (7)	27.04 (5)
February to August			
NE Brazil	154.00 (5)	107.60 (5)	28.60 (5)
SE Brazil	162.06 (16)	113.25 (16)	28.26 (16)
Bolivia—M. Grosso	157.80 (6)	109.60 (6)	27.68 (6)
S Paraguay	161.00 (5)	111.60 (5)	28.22 (5)
Corrientes	163.17 (23)	112.11 (22)	28.35 (22)
Misiones	163.89 (9)	111.22 (9)	27.86 (8)
Entre Ríos	158.67 (6)	107.80 (5)	28.07 (6)
Uruguay	159.00 (5)	108.17 (6)	27.51 (7)
SW Argentina	164.83 (6)	114.83 (6)	28.07 (6)

^a Samples arranged generally N to S, from *Colaptes campestris campestris* to *C. c. campestroides*. Sample sizes are in parentheses.

TABLE 18
MEAN MEASUREMENTS (IN MILLIMETERS) OF WING, TAIL,
AND BILL LENGTH IN FEMALE CAMPO FLICKERS^a

Sample	Wing Length	Tail Length	Bill Length
September to December			
Bolivia—M. Grosso	157.88 (11)	110.88 (11)	26.77 (11)
N Paraguay	—	107.20 (5)	—
S Paraguay	—	110.80 (5)	28.18 (5)
Corrientes	159.50 (6)	107.50 (6)	27.64 (5)
Misiones	162.00 (5)	109.25 (5)	27.76 (5)
R. G. do Sul	162.20 (5)	109.20 (5)	26.94 (5)
Buenos Aires	160.80 (5)	109.60 (5)	26.02 (5)
February to August			
NE Brazil	156.91 (13)	109.17 (10)	27.26 (11)
SE Brazil	158.20 (10)	109.75 (8)	28.83 (10)
Bolivia—M. Grosso	159.40 (13)	110.00 (13)	27.74 (12)
N Paraguay	158.20 (5)	—	28.98 (5)
C Paraguay	161.33 (6)	—	28.40 (5)
S Paraguay	161.00 (5)	107.00 (5)	27.58 (5)
Corrientes	162.25 (17)	112.50 (16)	28.04 (17)
Misiones	162.95 (20)	111.45 (20)	28.13 (20)
Entre Ríos	158.54 (13)	107.69 (13)	27.10 (13)

^a Samples arranged generally N to S, from *Colaptes campestris campestris* to *C. c. campestroides*. Sample sizes are in parentheses.

TABLE 19
ANALYSIS OF TARSAL LENGTH (IN MILLIMETERS) IN CAMPO FLICKERS^a

Sample	N	Mean	SE	SD	Range
MALES					
NE Brazil	5	29.04	0.40	0.90	28.2–30.5
SE Brazil	17	30.52	0.21	0.85	29.0–31.7
Bolivia–M. Grosso	15	30.25	0.31	1.11	28.2–32.4
NE Paraguay	6	30.73	0.80	1.96	29.7–33.4
N Paraguay	5	29.62	0.61	1.36	28.2–31.6
S Paraguay	5	31.46	0.43	0.97	30.3–32.6
Corrientes	13	30.30	0.32	1.14	27.4–32.0
Misiones	18	30.69	0.32	1.37	28.5–32.9
Entre Ríos	6	30.43	0.61	1.50	28.6–33.1
R. G. do Sul	7	30.49	0.42	1.11	28.9–32.2
Uruguay	10	30.58	0.30	0.94	28.8–32.0
SW Argentina	6	31.38	0.42	1.03	29.8–32.5
FEMALES					
NE Brazil	7	28.70	0.27	0.73	27.9–29.7
SE Brazil	10	29.88	0.25	0.80	28.3–31.0
Bolivia–M. Grosso	12	30.00	0.42	1.27	28.0–31.8
N Paraguay	5	30.74	0.80	1.79	29.1–33.6
C Paraguay	6	30.70	0.15	0.37	30.2–31.2
S Paraguay	7	31.44	0.57	1.51	29.1–34.0
Corrientes	9	30.85	0.45	1.34	28.1–32.4
Misiones	20	30.64	0.19	0.84	29.1–32.1
Entre Ríos	13	30.38	0.33	1.19	28.7–33.0
R. G. do Sul	5	30.80	1.02	2.28	29.7–32.0
Uruguay	7	31.04	0.32	0.86	29.6–32.1
Buenos Aires	5	30.88	0.32	0.73	30.0–31.6

^a Samples arranged generally N to S, from *Colaptes campestris campestris* to *C. c. campestroides*.

Symbols: N, sample size; SE, standard error of mean; SD, standard deviation.

above. The depth of the back bars was measured (penultimate dark bar on randomly selected feather from upper back) for each bird. No sexual difference was noted in this character. The bars tend to be broader in *campestroides*, although overlap is great.

GEOGRAPHIC VARIATION

Geographic variation in this species, compared with *C. melanochloros* and *C. auratus*, is very limited. Indeed, the essential fact resulting from this phase of the study is the great uniformity of *C. campestris*, other than in throat color. No characters were found to define further *Colaptes campestris campestris* and *C. c. campestroides*, much less any other proposed races.

Variation in mensural characters (see tables 17, 18, and 19) is least in bill length ($3\frac{1}{2}$ to $4\frac{1}{2}$ per cent among various sample means), somewhat greater in wing length and in tail length

(sample means vary 4 to 7 per cent in each), and is greatest (7 to 8 per cent) in tarsal length. Variation of less than 10 per cent in these measurements is not considered significant in birds exhibiting individual variation often exceeding 10 per cent, as it does in Campo Flickers. Furthermore, the variation bears no relation to the recognized races of this species. The patterns instead show: a tendency for lesser measurements in the far north (Beni, Bolivia, and north-eastern Brazil), and for greater measurements in the extreme south (southwestern Argentina); and a tendency for greater measurements in birds of the Brazilian highlands, and adjacent, largely forested areas, involving both *C. c. campestris* (São Paulo, Paraná) and *C. c. campestroides* (Misiones, Corrientes, Rio Grande do Sul).

Extreme short wing measurements of *C. c. campestris* are 147 mm. from Piauhy, 148 mm. from Beni, Bolivia, and 143 mm. from Buena

Vista, Santa Cruz. High wing measurements for the same areas, sexes, and seasons are 160 mm. for a Piauhý male, and 161 mm. for a Sara, Santa Cruz, Bolivia, male. Only about 10 individuals of *campestris* measure 150 mm. or less, and none of *campestroides* do so. The greatest wing length achieved by *campestris* is 173 mm. (two males from São Paulo); the few individuals of *campestroides* with wings exceeding 170 mm. in length are birds from southern Paraguay (171 mm.), Misiones (171 mm.), Río Negro (172 mm.), and Córdoba (177 mm.). Data for length of the outer (tenth) primary, and for primary 9 yield results similar to those for overall wing length.

Extreme short-tailed specimens of *campestris* come from Beni and Santa Cruz, Bolivia (94, 96, 98 mm.). The only *campestroides* specimen measuring under 100 mm. in tail length is from Misiones (99 mm.). The longest-tailed *campestris* (117, 122 mm.) are from São Paulo, and the longest-tailed *campestroides* (121, 121 mm.) come from Córdoba and Río Negro, Argentina. There is a tendency for *campestris* to have relatively longer tails than *campestroides*.

Small extremes for bill length in *campestris* are: 25.5 mm., Bahía; 24.6 mm., São Paulo; 25.5 mm., Santa Cruz, Bolivia; and 23.7 mm., Mato Grosso. Similar extremes for *campestroides* are: 24.2 mm., Entre Ríos; 25.5 mm., Chaco, Argentina; 24.5 mm., Buenos Aires; and 23.8 mm., Misiones. Only 13 specimens of *campestroides* exceed 30.0 mm. in bill length, and but one (from southern Paraguay) exceeds 31.0 mm. Twelve specimens of *campestris* exceed 30.0 mm. in bill length, five of them (from Bahía, northern Paraguay, Mato Grosso) exceed 31.0, and one of these exceeds 32.0 (32.5 mm., northern Paraguay). Perhaps significant is the fact that five of the seven specimens exceeding 31.0 mm. in bill length, including the only two birds exceeding 32.0 mm. (one of these is a central Paraguayan possible hybrid, with a bill length of 32.7 mm., the longest-billed specimen of *C. campestris* that I have seen, discussed below), come from Paraguay, where *campestris* and *campestroides* meet and interbreed. There seems to be no geographic pattern of variation in bill length.

Data for tarsal length (table 19) indicate no clear pattern of geographic variation. There is a tendency for shorter legs in the far northern range of the species (northeastern Brazil), from whence comes the only sample (females) lacking

birds measuring over 30.0 mm. in tarsal length.

A tendency is evident toward greater tail/wing ratios in *campestris* (averages 0.685 to 0.710), compared with *campestroides* (averages 0.670 to 0.695). It is not certain whether this reflects longer tails or relatively shorter wings on the average in *campestris*.

There is little variation in back barring. *Colaptes campestris campestris* samples (22 of them) average between 4.10 and 5.15 mm. in depth of back bars. Samples (15 in all) range from 3.75 to 5.13 mm. in depth of back bars of *C. c. campestris*, showing greater variation. Most of this variation is due to the deeper back bars of highland southeastern Brazil birds, all four samples of which average more than 4.5 mm. (one Bolivian and one north Paraguayan sample also average above this figure). Eight samples of *campestris* average less than 4.25 mm.; the only *campestroides* samples averaging below 4.25 mm. in back bar depth are from southern Paraguay, adjacent to the zone of interbreeding with *campestris*.

Patterns of geographic variation were not noted for other characters, except throat color discussed below.

HYBRIDIZATION

Colaptes campestris campestris and *C. c. campestroides* differ essentially in throat color, which is somewhat variable, especially in the former. Other slight differences exist as tendencies, e.g., in tail/wing ratio. The shift in throat color from the black, or almost black throat of *campestris* to the essentially white throat of *campestroides* occurs over a short distance, and adequate samples are not available from the region where the shift occurs. Nevertheless, available evidence suggests that the shift takes place through a narrow hybrid zone, and that slight introgression is occurring through at least one part of this hybrid zone.

The evidence necessary to show that hybridization and introgression are involved in patterns of variation usually is of two types. The first is the geographical orientation of the character clines, such that convergence occurs where morphologically (often physiologically as well) divergent populations geographically approach each other. The second is enhanced variation in the populations occupying the area of contact, or overlap. An additional related factor is that hybridization involves secondary contact

TABLE 20
THROAT COLOR SCORES OF ADULT CAMPO FLICKERS^a

Sample	N	Scores								Per cent below 4	Per cent above 0	
		0	0+	1	1+	2	2+	3	3+			4
MALES												
C, E Brazil	55	—	—	—	—	1	2	11	19	22	60	100
N Paraguay	16	—	—	—	—	—	—	4	8	4	75	100
Hybrid zone	3	—	—	—	—	2	—	1	—	—	100	100
S Paraguay	14	9	1	1	1	1	1	—	+	—	100	36
Corr., Mis., S Brazil	53	34	11	6	2	(1)	—	—	—	—	100	36
Uruguay; W, S Argentina	33	29	3	1	—	—	—	—	—	—	100	12
FEMALES												
C, E Brazil	51	—	—	—	—	3	7	14	11	16	69	100
N Paraguay	20	—	—	—	—	—	2	6	10	2	90	100
Hybrid zone	6	—	1	—	2	—	—	1	2	—	100	100
S Paraguay	23	10	5	2	5	1	—	—	—	—	100	55
Corr., Mis., S Brazil	56	42	12	2	—	—	—	—	—	—	100	25
Uruguay; W, S Argentina	34	30	2	2	—	—	—	—	—	—	100	12

^a All adults except for one immature marked + in body of table. Hybrid zone sample from central Paraguay and Formosa except one male from Misiones (shown under Misiones also, in parentheses). Samples arranged from *Colaptes campestris campestris* (above hybrid zone) to *C. campestris campestris* (below hybrid zone). N, sample size.

between two or more formerly geographically isolated (or essentially isolated, i.e., tenuous contacts over great distances may allow differentiation) forms. These contacts often occur in ecotones, and several different pairs of organisms (plants, animals) frequently hybridize in the same region. These hybrid zones coincide roughly with zones of contact or partial overlap among closely related, but fully evolved species. Because of the varying action of natural selection within and adjacent to hybrid zones, it is important to treat as many characters as one has to work with. Certainly it is true that a hybrid zone can be defined better using many characters, or several characters than it can with few, or only one. In the present case, only one such character is available.

I infer from the data presented below that hybridization is occurring. That the variation observed is indeed due to hybridization is based on these data and other points. One of these is the likelihood that *campestris* and *campestris* are in tenuous secondary contact, and they have been geographically isolated. Continuous open country connecting the two forms is extremely limited, and was even more limited before man came into the region. The pantanal of Paraguay seems today to be the major open

or semi-open area connecting these forms that did so in the past as well. Otherwise, chaco woodland (western Paraguay) and forest barriers (eastern Paraguay, Misiones, Santa Catarina) effectively separated these forms until recently. In Misiones I have seen the gradual opening of the subtropical forest, allowing infiltration of *campestris* into central Misiones, where it appears likely to be meeting southward infiltrating *campestris* for the first time in that region. The cutting of trees in the Chaco, in eastern Paraguay, in northern Rio Grande do Sul, and in southern Santa Catarina also may be facilitating contact in those regions. Another point is that the *campestris*-*campestris* contact occurs in an area where other forms are in secondary contact, namely in the region where chaco woodland, pampas, and subtropical moist forest form ecotones. Among these other forms are the hybridizing groups of *Colaptes melanochloros*, discussed above, and *Celeus lugubris* and *Celeus flavescens* whose interaction is unstudied as yet.

Within the range of *campestris* north and east of Paraguay and of Santa Catarina only 35 per cent (38 of 106) of the specimens have a fully black throat. Variation away from this condition (table 20) involves chiefly a few white

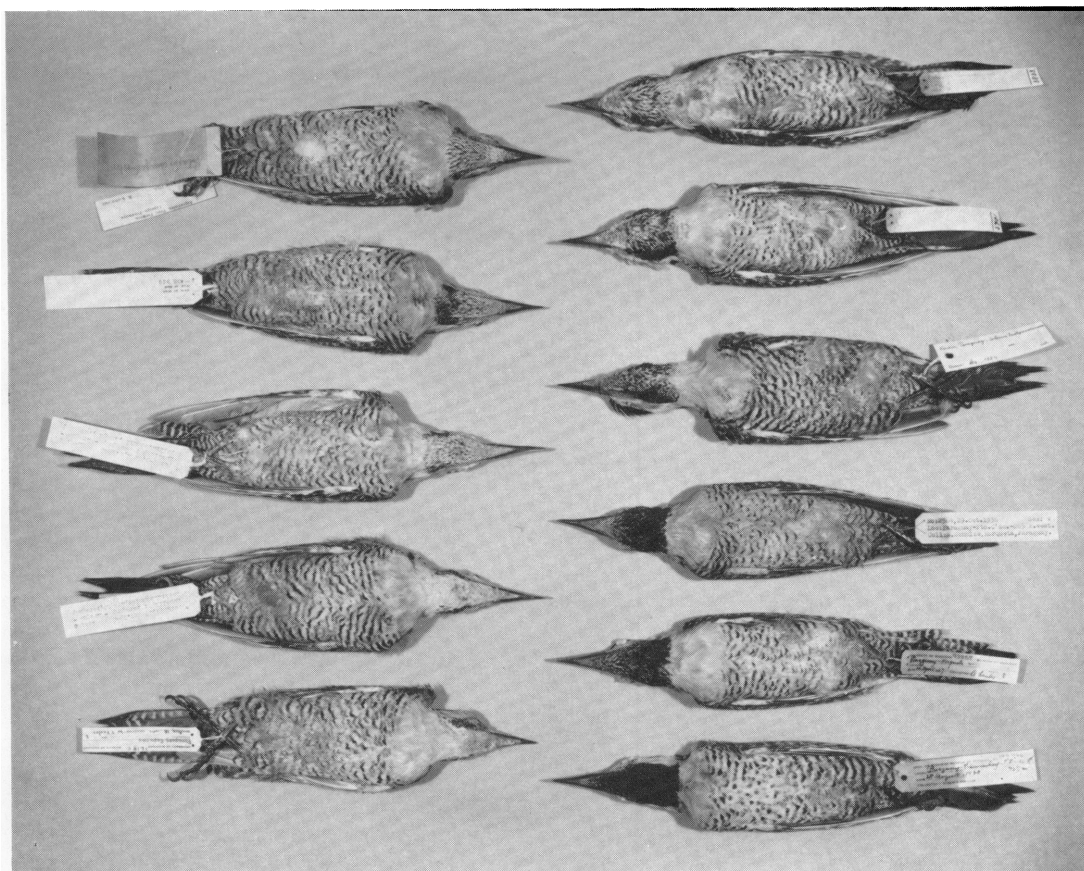


FIG. 12. Specimens of *Colaptes campestris* showing throat color variation in racial hybrids of *C. c. campestris* $\times$ *C. c. campestroides*. Observe variation from white throat, lower left, clockwise through intermediate stages to black throat, lower right. Specimens from lower left upward are (throat color scores in parentheses): UMMZ 1618c, Sapucay, Paraguay (0); UMMZ 111389, Aregua, Paraguay (0+); UMMZ 111390, Aregua (1); UMMZ 105359, "Riacho Negro," Paraguay (1+); and NMM 27-1235, Lapango, Formosa (1+). From the top right down are: UMMZ 93362, E Rosario, Paraguay (1+); UMMZ 93361, Rosario (2); NMM 59-307, Colonia Independencia, Paraguay (2); UMMZ 92851, 265 km. W Puerto Casado, Paraguay (3); UMMZ 93357, Horqueta, Paraguay (3); and at the bottom UMMZ 100066, Capitán Bado, Paraguay (4). Note individual variation in ventral barring.

spots in the black throat (28 per cent of birds) and a scattering of such spots on a largely black throat (another 23 per cent). Some birds deviate more strongly from the black throat, scoring 2+, and a few (1 male, 3 females) have the throat so mixed with white as to be half white and half black (score 2). Two of these extreme variants come from so far away from the range of *campestroides* that introgression cannot be held directly responsible for them (indirectly, this is possible), but the others come from São Paulo (Ypanema) and Paraná (Rio Baile), conceivably

near enough the range of *campestroides* for introgression possibly to be effective. Thus the scores of *campestris* specimens range from 2 to 4; 88 per cent score 3 to 4 (see fig. 12).

Specimens from northern Paraguay (table 20) represent the following localities: Concepción, 110 km. W Concepción, Horqueta, Río Siete Puntas, Nueva Germania, 40 km. SW Capitán Bado, Cerro Galban, Casilota, San Luís de la Sierra, W of Puerto Pinasco, Puerto Pinasco, W of Puerto Casado, Puerto Guaraní and Zanja Moroti. Also included in the table

is a lone bird from Santa Catarina (Arroyo Verde, throat score 3). This sample contains birds from adjacent to the contact zone with *campestris*. Although the sample is not very large, the proportion of lower scoring birds is greater (75 per cent of males, 90 per cent of females) and that of all black-throated flickers is less (17 per cent overall) than in birds from central and eastern Brazil. This could be due to introgression. Note that females of *campestris* vary more toward *campestris* in this feature than do males.

The samples of *campestris* were grouped according to distance from the range of *C. c. campestris*. The southern Paraguay combined sample includes birds from an area immediately adjacent to a known zone of contact (central Paraguay) with *campestris*. A second combined sample contains birds from Corrientes, Misiones, and Rio Grande do Sul, areas near the contact (Paraguay) or possible contact (northern Misiones, Santa Catarina) between the two races. Finally, a third sample includes birds from Uruguay, and Argentina from Entre Ríos, Chaco, and Santiago del Estero south to Patagonia, that is from the area away from possible contact with *campestris*. Examining the last sample first for throat color (table 20), we find much less variation from the typical white throat of *campestris* than there is variation away from a black throat within *campestris*. Only 12 per cent of the specimens show a few spots (score 0+) to scattered black spots (score 1). Of the three flickers scoring 1, one comes from Buenos Aires, far from *campestris*; the other two are from Entre Ríos, not beyond possible effects of introgression.

The large, pooled Corrientes-Misiones-Rio Grande do Sul sample contains more birds tending toward *campestris* than does the more southern sample. Over twice as many females and three times as many males score 0+ or more, and two males even attain a score of 1+ (see below for a Misiones bird scoring 2). Chi-square tests show this difference to be significant at the $P=0.99$ level. Note that females are less likely to show black in the throat than are males. This may reflect a sex-linked genetic difference, as females of black-throated *campestris* more readily show white in the throat than do males.

The southern Paraguay sample is small, but the proportion of birds scoring above 0 probably is greater (36 per cent, same in males, but 55 per cent versus 25 per cent for females, latter

significant by Chi-square test) than in the Corrientes-Misiones-Southern Brazil sample. Furthermore, six females and two males exceed the variation in all other *campestris* by scoring 1+ and 2 (females), and 2 and 2+ (males). All of these high-scoring birds come from the northernmost localities, those (Sapucay, Asunción, Aregua, Pilcomayo River) closest to the area whence come the hybrids.¹ The Sapucay sample contains two males scoring 0 and 2+, and four females scoring 0, 1+, 1+, and 2. I believe that the high scores of southern Paraguay birds reflect the effects of introgression from *campestris*. Localities represented by this sample, other than those mentioned above are: Colonia Nueva Italia, Colonia Independencia, Villa Rica, Encarnación (several localities nearby), Capitán Meza, and Colonia Pfannl, in southern Paraguay; La Urbana, Lapango, Clorinda, and Río Pilcomayo, in Formosa; and Escalante along the Pilcomayo River in southwestern Paraguay. Another locality included is Ibitimi or Ybytí, presumed to be that near Itapé and Villa Rica rather than Igatí (on the Arroyo Itapé!) farther north in eastern Paraguay (the specimen involved is BM 1905.10.12.132, taken by W. Foster, who worked in the Sapucay-Villa Rica area in 1903–1904).

The northernmost localities whence come birds scoring 0 are: the Pilcomayo River in several places; Asunción, Aregua, Sapucay, Ibitimi, and Capitán Meza in eastern Paraguay; Puerto Piray, and 14 km. SW San Pedro, central Misiones (white-throated birds observed uncommonly in newly cultivated areas north to near Puerto Libertad, just south of W. Partridge's collecting locality at Arroyo Uruguay; Partridge obtained no Campo Flickers at that locality despite months of general collecting); and Passo da Entrada, São Francisco da Paula and Lagoa do Forno in northern Rio Grande do Sul. The southernmost localities for birds scoring 4 are: Horqueta and Capitán Bado in Paraguay, and various localities in southern Paraná. An immature bird with a virtually black throat (between 3+ and 4) comes from Pastorea, east of Caaguazú (about 182 km. E Asunción), Paraguay, somewhat south of where adults scoring 4 have been taken.

Localities in the zone between those sites

¹Many of the localities mentioned here are shown on figure 3, although that figure chiefly treats localities for *C. melanochloros*.

from which 0-scoring flickers and those from which 4-scoring flickers are known represent only central Paraguay. One locality is the uncertain "Riacho Negro" site discussed above under *Colaptes melanochloros*. The three birds in the sample represent the dates August 1 to August 6, 1939, within the period when specimens probably were collected elsewhere, perhaps in central eastern Paraguay. These flickers score 1+, 3+, and 3. Five specimens (see fig. 12) obtained 14 to 25 km. E Rosario score 0+, 1+, 2, 3, and 3+, thus virtually bridging the gap between white-throated and black-throated extremes. Included in the "hybrid zone" sample in table 20 is a male flicker with a throat score of 2 collected south of Fracrán, in the central Misiones highlands in October, 1967. Birds from south of Fracrán do not score over 1 (only five of 50 southern Misiones birds attain a score as high as 1). Only one bird was observed in the Misiones highlands to the north of Fracrán, namely a single female (scoring 0) taken near San Pedro. Clearing of forests is progressing rapidly in this region, as it is along the Upper Parana River. It is likely that sporadic meeting and hybridization is occurring between *campestris* and *campestroides* infiltrating open, cultivated lands in central and northern Misiones. Birds scoring 2 are otherwise known in *campestroides* only within and immediately adjacent to the hybrid zone in central and southern Paraguay. It appears that Campo Flickers are scarce in the forest region of northern Misiones and southwestern Paraná. Studies are needed to establish the nature of contacts between the two forms of this species in this region.

Farther east, a dearth of specimens complicates the picture also. It is clear that *Colaptes campestris campestroides* occupies all of Rio Grande do Sul, and it probably extends into the southern edge of Santa Catarina (probably especially coastally) as well. The highland area extending in an east-west direction across Santa Catarina may today prevent, or in the past may have prevented contact between *campestroides* and *campestris*. The single specimen (AMNH 314328) from Santa Catarina unfortunately represents the northern fringe (Oura Verde) of that state. Its score of 3 places is well within the range of variation of *campestris*, especially as it is a female; of course it could come from a hybrid zone as well.

CONCLUSIONS

An ill-defined hybrid zone occurs between *C. c. campestris* and *C. c. campestroides* from the Paraguayan chaco across central eastern Paraguay, the northern edge of Misiones, and eastward across Santa Catarina. Extensive, continuous forest probably effectively isolated *campestris* from *campestroides* between eastern Paraguay and the Atlantic Ocean, until the forests began to be cleared on a large scale, mainly since European man entered the region. Likewise, the Chaco may have contained little or no natural grassland (even today one can cross from Formosa to Jujuy through chaco woods that are essentially continuous, and surely they were in the recent past) prior to man's cutting of trees, cultivation of land, burning practices, and pasturing of cattle in those woodlands. The pantanal area surrounding the Paraguay River probably afforded the only major area of suitable open habitat allowing contact between the two forms prior to settlement by European man. It is conceivable that forested swamps and extensive marshes prevailed in this area in the recent past, and that drier grassland developed only recently, providing a savanna-pampas corridor. There seems to have been ample opportunity for geographic isolation of *campestris* and *campestroides*, and we seem to be witnessing today an expanding area of secondary contact between them. From the very small sample available, it appears that these closely similar forms interbreed in a narrow hybrid zone in Paraguay, and sporadically hybridize in the area of contact elsewhere. The convergent pattern of intermediacy of their throat color (fig. 12), the lack of the extreme parental phenotypes, and their variability suggest that hybridization is complete, that is, a true Hybrid Zone (Short 1969a) exists in Paraguay.

The small extent of the hybrid zone probably reflects the limitation on contact between these forms by extrinsic factors, namely, topographic and vegetational features of the environment. We are hampered in appraising their interbreeding by the dearth of characters distinguishing them. Indeed, the similarity of the two races makes it unlikely that they are hampered in interbreeding where the opportunity exists to do so. Of course there may be strong selection acting to limit the flow of genes responsible for throat color (or the genes with which those

determining throat color are associated), whereas other genes and gene combinations may be passing more freely through the zone. The variability of *campestris* in throat color indicates that the color of the throat patch itself is not strongly maintained by selection, and hence it probably is not crucial in pair-formation or other behavior. It is clear that the two forms are interbreeding, and there is no apparent barrier to such interbreeding. Selection of genes and gene combinations through a hybrid zone differs not at all from that occurring in all zones of intergradation, and it has no bearing on the taxonomic status of the forms involved (of course it does bear importantly on the structure of the gene pool, and the evolution of the species).

There is no major morphological difference between *campestris* and *campestroides* in features other than throat color. All other differences represent slight tendencies, the subspecies overlapping greatly. Individual variation is great within each of the forms, and the two are so similar to each other, that no other races are

recognizable. The only other subspecies that has been generally recognized is *Colaptes campestris chrysosternus* (Swainson), from northeastern Brazil (see Peters, 1948). Although birds from that area tend to be slightly smaller, and less barred below, they greatly overlap with specimens to the south and west (*campestris*). Also similar tendencies exist in northern Bolivia and Mato Grosso. It seems best to note these tendencies, but not to recognize them by erecting new subspecies or maintaining weak races that have been named earlier. Mees (1968) has commented recently on *chrysosternus*, and he also found it too weakly defined to recognize nomenclaturally. Thus, *chrysosternus* becomes a synonym of *campestris*. The races of the Campo Flicker are:

(1) *Colaptes campestris campestris* (Vieillot), 1818

Type locality, "Paraguay."

(2) *Colaptes campestris campestroides* (Malherbe), 1849

Type locality, "South America."

SOCIAL BEHAVIOR

IN THIS SECTION are documented the habits, vocalizations and instrumental signals, and displays of South American flickers. I present and discuss salient features of their life history useful in appraising their relationships. A secondary purpose is to encourage others to fill in the gaps in our knowledge of these flickers. Subsections below treat in order general habits (e.g., preferred habitats, nesting sites, breeding seasons, foraging behavior) of each species, instrumental signals and vocalizations, visual displays, and pair formation and possible isolating mechanisms.

HABITS AND HABITATS OF THE FLICKERS

For each of the South American flickers I attempt to treat what I have learned of the preferred habitats, foraging behavior and com-

petitors, foods, and nesting sites and breeding seasons. I have also included data on the condition of gonads, soft part colors, and other information derived from the specimens which were collected.

Colaptes atricollis

The Black-necked Flicker was observed briefly during late August, 1968, in the Santa Eulalia Valley 7 km. NE Chosica (east of Lima), Peru, at an elevation of about 1100 m. Its habitat (fig. 13) was an arid valley extensively cultivated with orchards and gardens, and with some tiny remnants of natural woods. About 100 m. above the valley floor all continuous vegetation gave way abruptly to barren, boulder-strewn slopes. Columnar cacti attaining a maximum height of 4 m. were scattered about the rocky slopes, and ravines contained clustered cacti of several species and acacia-like



FIG. 13. Habitat of *Colaptes atricollis* in Santa Eulalia Valley, east of Lima, Peru, elevation about 100 m. The flickers foraged chiefly in the cultivated trees in the valley. An old nesting cavity and roosting hole of a male was situated in the telegraph pole (center). Note barren, desert slopes above valley and abrupt shift at point where irrigation commences. The foreground boulder and cactus slope continues to the left and behind the photographer. Flickers were not observed in the desert itself during my brief visit.

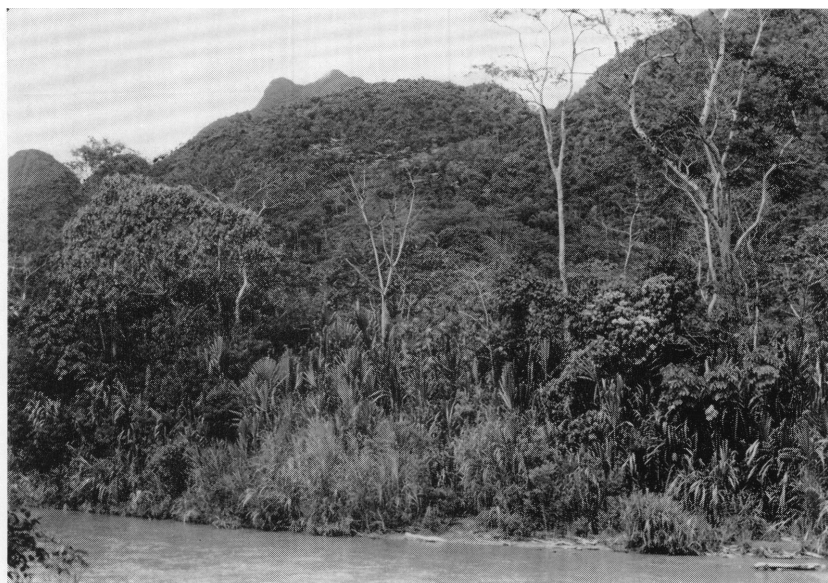


FIG. 14. Second-growth forest along the Huallaga River at Tingo María, Peru, habitat of *Colaptes punctigula*. Elevation about 700 m. The flickers drank at the edge of the river and foraged in open spaces along it. The birds were not found on the forested slopes.

trees. Nowhere in the valley does the natural vegetation of the slopes become sufficiently dense to impede progress in walking (although the boulders and jagged smaller rocks make walking difficult). The desert presumably constitutes the original habitat of this species, although it undoubtedly occupied the scattered wooded valleys as well. An inland race occupies the scrub desert of the upper Marañón Valley.

In this setting I studied a pair of these flickers. The birds occurred predominantly in the cultivated valley, and indeed only once was an individual seen (perched in a cactus) above the border of desert and irrigated land. Although but one pair was observed, one other bird was heard, and telephone poles beside the road throughout the Santa Eulalia Valley bear holes testifying to the occurrence of this woodpecker. No other species of woodpecker is known to occur in the lower western Andean slopes of the Department of Lima (Koeppke, 1964).

The flickers had nested prior to my visit, probably in late June and July. A single, late-August male specimen had regressing testes (left 7 by 5 mm. with a 4 mm. curved tip, and right 4 by 3 mm.) and a refeathering brood

patch. This male was leisurely engaged in excavating a presumed roosting cavity in a telephone pole on the slope (but within the irrigated area). The male visited the pole casually but regularly over two days for a few minutes each time. On three occasions it devoted five minutes to excavating and tossing out wood chips.

The pair were observed foraging only in trees such as apple and a leguminous species. Several instances were noted in which the birds flew up from a tree base, indicating that they may have been foraging on the ground. Indeed, fresh soil on the bill of the male I collected suggests terrestrial foraging. No foraging was observed in the desert. Arboreal foraging was by probing and picking with occasional tapping especially of dead branchlets. The stomach of the single specimen contained masses of ants, ant pupae, and larvae. Thus the Black-necked Flicker tentatively must be regarded as an ant-foraging woodpecker.

No displays were observed (but see section on vocalizations). The adult male specimen weighed 89.8 gm. Its irides were chestnut, and its legs were pale green-gray.

Colaptes punctigula

The Spot-breasted Flicker was studied during mid-August, 1968, in the area within 16 miles north of Tingo María, Huanuco Department, Peru. Its habitat there is the forest edges, second growth forest (fig. 14), cultivated areas with sufficient arboreal vegetation, and swamp edges (see fig. 2 in Short, 1970a, for a photograph of the last). In such situations these flickers were nesting at the time of my studies.

Foraging birds were observed on the ground in open places such as pastures and in various trees. Ground foraging is in the manner of *Colaptes melanochloros* and *C. auratus*. It involves hopping about the ground, probing into the ground and bill flicking, which clears an opening into the soil usually in places where ants have congregated. Arboreal foraging consists of light tapping and especially probing and other forms of surface-gleaning. No prolonged tapping or excavating was noted. The stomachs of two specimens contained only the remains of ants (large numbers of ants, pupae, larvae, and some eggs).

Within its habitat in eastern Peru, various other species of woodpeckers were observed (Short, 1970a); additional species occur with it in other portions of its range. Because of the small size of *punctigula* and its ant-foraging habits, only a few sympatric species of woodpeckers are potential competitors. Possible competitors for food include species of the *Celeus undatus* group (including *undatus*, *grammicus*, and *loricatus*) and various species of *Piculus* (e.g., possibly *rubiginosus*, *flavigula*, *leucolaemus*, and *chrysochloros*). Its range does not meet that of any other species of *Colaptes*. Nest-site competition may occur with any generally small- to medium-sized, sympatric woodpecker, but data are lacking on this matter.

Nesting had commenced by mid-August northeast of Tingo María. Favored nest sites apparently are stubs along the edges of forest, or in pastures. One pair frequently were observed in displays concentrated in four or five trees isolated within a pasture. Three of these trees were partly dead and one bore an old woodpecker hole perhaps of this pair of flickers. A pair were collected beside their nest cavity 10 feet above ground in a wispy, 18-foot high dead tree measuring 5 inches in diameter at breast height. This tree was situated in a swamp (fig. 2 in Short, 1970a). On August 17 nesting was

under way, but egg-laying had not commenced. The female, taken near the nest in the swamp, had an enlarged ovary (10 by 7 mm.) and ova up to 3 mm. in diameter. Its mate had testes measuring 8 by 3 mm. with a 2 mm. curved tip (left testis) and 4 by 2 mm. (right testis). Both flickers had well-developed brood patches.

Displays and vocalizations of this species are described below. The two specimens weighed 79 gm. (female) and 75 gm. (male). Both had rufous-brown irides and yellowish green-gray legs and feet.

Colaptes melanochloros

I studied Green-barred Flickers in Corrientes, Misiones and southwestern Buenos Aires provinces, Argentina, from September to December, 1967, and in Formosa and Santa Fe provinces, Argentina, in September, 1968. The subspecies I studied included *melanochloros* of the *melanochloros* group, and *nigroviridis* and *leucofrenatus* of the *melanolaimus* group. I also observed hybrids of the *melanochloros* and *melanolaimus* groups. The habitats of this species vary considerably, and they include: savannas (*nattereri* and *melanolaimus* group), chaco (*melanolaimus* group, fig. 15; for very different aspects see Short, 1968a, fig. 5, and Short, 1971e, fig. 2), and caatinga (*nattereri*), or arid woodlands, desert scrub (*melanolaimus* group), pantanal (palm savanna and marshes), riparian forest and woods, and both upland and lowland (figs. 16, 17) subtropical moist forest (*melanochloros* group). Although inhabiting fairly open country, as in the pampas, this flicker requires trees for nesting and for some or most of its foraging, for it is found only in the vicinity of trees. The forest-dwelling *C. m. melanochloros* particularly favors areas of bamboo growth.

Arboreal foraging involves much probing and surface gleaning for ants. The birds occasionally may peck lightly while feeding, but pecking rarely or never is prolonged. Individuals feed on ants in ant-excavated branches of trees, much in the manner of *Celeus* woodpeckers, that is, by using the bill to break through the surface and then extracting insects with the tongue for many minutes. All kinds of trees, including palms and bamboos, and all sizes are utilized for foraging. Although the flickers feed at all elevations they frequently are encountered within 3 or 4 m. of the ground. I do not know

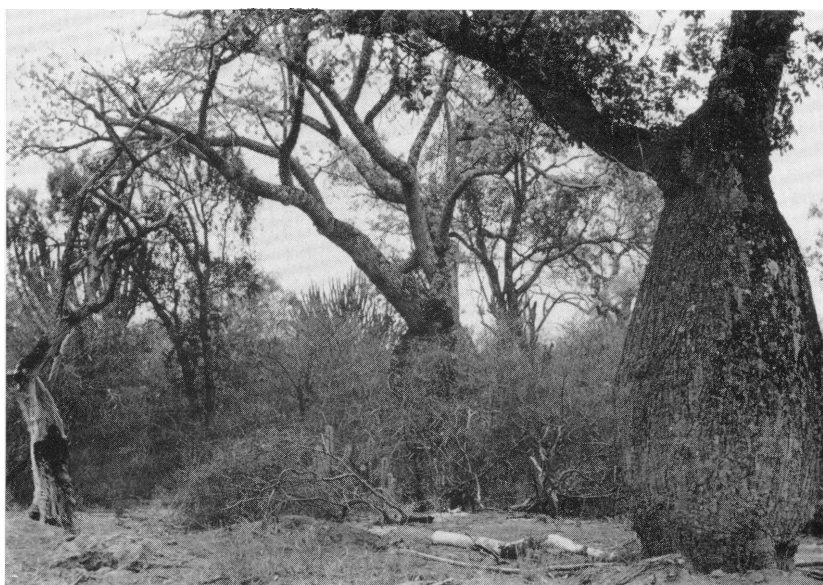


FIG. 15. Dry chaco woodland near Pozo del Tigre, Formosa, habitat of *Colaptes melanochloros nigroviridis*. Elevation about 110 m. Photograph taken in September, 1968. Flickers forage arboreally and on the ground in open places such as this (foreground).



FIG. 16. Second-growth forest habitat of *Colpates melanochloros melanochloros* near San Pedro in the Misiones, Argentina, highlands. Elevation about 400 m. The opening of a nesting cavity of a pair of these flickers is visible in the stub in the center of the photograph.



FIG. 17. Clearing near Puerto Libertad and Upper Parana River, Misiones, elevation about 50 m. Habitat of *Colaptes melanochloros melanochloros* (forest, background), and invading *Colpates campestris campestris* (and *campestris*?) which is occupying such clearings. Note evergreens planted in foreground.

to what extent the *melanochloros* group forages terrestrially, but hybrids of the *melanochloros* × *melanolaimus* groups and various races of the *melanolaimus* group feed on the ground regularly (in cases perhaps predominantly, at the season in which they were observed). In five or six instances (involving *nigroviridis*) birds flushed from the ground went to the ground several times thereafter, following my persistent intrusion. That is, an alarmed bird would fly from the ground to either a neighboring or distant tree, pause for a few moments, then descend to the ground and resume foraging; if disturbed again, it might repeat this several times, although pausing for increasingly longer periods before descending. I have seen individuals of *Colaptes auratus* perform similarly. Terrestrial foraging, frequently in company with *Colaptes campestris* (see Short, 1969b), involved hopping about, usually in areas where ants could be seen (e.g., on obvious anthills). The progression of *melanochloros* on the ground, either by long bounds or short hops, is like the hopping of *C. auratus*, which it otherwise resembles very much (i.e., in flight, size, coloration). I have observed *C. melanochloros* dust-bathing on a dirt road in Misiones, Argentina.

The main food, indeed almost the only food of these green flickers, consists of ants. The contents of 40 stomachs from birds of various localities were examined. In only one could I find food items other than ants, namely the remains of two spiders. The stomach containing the spiders otherwise was filled with ants. All other stomachs, and the esophagus of many of the birds as well, contained ants, ant eggs, ant pupae, and ant larvae. William Brown kindly examined the contents of two stomachs of birds collected north of Ituzaingó, Corrientes. He found in the first of these the following items: females and workers of two or more species of *Crematogaster*; soldiers, callow males, pupae, and larvae of *Camponotus* sp.; and a worker of *Paracryptocerus*. In the other stomach were: mainly *Camponotus* of three species, including brood (hence taken from nest); a worker of the *Camponotus abdominalis* group; workers of *Crematogaster (brevispinosus)* group; and soldiers and workers of the *Myrmobrachys* subgenus of *Crematogaster*. Except for the strictly arboreal *Paracryptocerus*, the ants that were taken represent arboreal-terrestrial groups, that is, those that nest in trees or on (in) the ground and also forage in both sites (W. Brown, *in litt.*). Both

birds involved in this detailed stomach analysis were collected while foraging in trees.

The Green-barred Flicker probably is allopatric with other flickers except for *C. campestris*, with which it is broadly sympatric. The forest-inhabiting forms (chiefly *C. m. melanochloros*) are ecologically separated from *campestris*, but in savanna and woodland formations the two flickers overlap, at least in the vicinity of trees. Terrestrially foraging Green-barred Flickers may forage in proximity to Campo Flickers, perhaps deriving benefits from association with their more terrestrially adapted relative (Short, 1969b). There is a possibility of limited contact with the Andean Flicker in upland valleys of Bolivia and northwestern Argentina, and with the Spot-breasted Flicker in Mato Grosso or Bolivia, and the Green-barred Flicker may have been in contact with the Chilean Flicker in the upper Limay River region at one time. However, definite evidence for sympatry with these three species is lacking at present. Thus, possible competition is limited to the Campo Flicker. There may exist limited competition for food between Green-barred and Campo flickers in the vicinity of trees, and possibly for nesting sites, although Campo Flickers utilizing trees for nesting invariably choose trees immediately adjacent to open country. It is conceivable that terrestrial foraging in Green-barred Flickers is most pronounced during their breeding season. In this case, since the breeding season probably coincides with the maximum abundance of ants, competition for superabundant ants may be limited or nonexistent. At other seasons the Green-barred Flicker may avoid competition with the Campo Flicker by foraging mainly in trees. Data are lacking to establish this. It is noteworthy that large southern specimens of *C. m. leucofrenatus* closely approximate in size the Campo Flickers with which they are sympatric. Elsewhere, Green-barred Flickers are distinctly smaller than Campo Flickers.

The breeding season commences in September for southern races, i.e., *melanochloros*, *leucofrenatus*, and *nigroviridis*, and young in the nest are known as late as January (Uruguay; Wetmore, 1926). Nesting sites (fig. 16) are in dead stubs of diverse trees (including palms, probably bamboo) at heights varying upward from 2 m. Occasionally, or locally, nests may be constructed in cacti, as possibly in Salta, Tucumán, and highland Bolivia, or in telegraph poles, as in

southern Buenos Aires Province where *leucofrenatus* occupied woods (see photograph, fig. 5 in Short, 1968) having trees generally too small for nesting purposes. Nests of the ground-foraging races often are placed in trees at the edge of woods, that is, overlooking open country. Four partly developed young were taken from a nest 5 m. in an ornamental tree beside a ranch house 30 km. west of Ituzaingó, Corrientes, on October 20. A nest containing four eggs about one-third incubated was found 6 m. in a dead tree near Itá-Ibaté, Corrientes, on October 31. Nest excavation in palms was under way in late September in Formosa. In southern Buenos Aires Province a male excavating a nest in a telephone pole on December 2 was taken. The condition of the gonads of specimens collected there indicates that eggs would have been laid in mid-December. Fledged young were seen as early as October (juvenile female taken with parents in bamboo beside nest 4 m. in tree on island in Parana River near Ituzaingó, Corrientes, on October 26). All adult birds collected in Corrientes and Misiones during September to November, in Formosa during September and October, and in southern Buenos Aires in early December, had enlarged gonads. The shortest testes measured were 6.5 mm. (left) and 4 mm. (right), and no ovary was less than 5 mm. in diameter. All adults had a well-developed brood patch.

Information concerning the weights of the adult specimens is presented in the taxonomic section. Ranges were from 106 to 150 gm. for Misiones, Corrientes, Santa Fe, and Formosa adults, and from 155 to 168 gm. for southern Buenos Aires adult flickers. An exception is a female taken on October 1 near Mocoví, Santa Fe, that weighed 165 gm.; this bird had a much enlarged ovary (18×11 mm.), and ova (to 5 mm.), and was about to lay eggs. The fledgling from Corrientes weighed 119 gm., and three (the fourth was not weighed) moderately developed nestlings from Corrientes mentioned above weighed 58.9, 56.7, and 52.8 gm.

Eye color in the Green-barred Flicker varies, but is always some shade of brown; there is variation in the presence and extent of orange-red, the eyes sometimes appearing dark brown, at other times red-brown, and occasionally chestnut. The bill is invariably black, and the legs gray, usually pale, often showing a green or yellow-green cast. Other features of behavior are discussed below, and information about

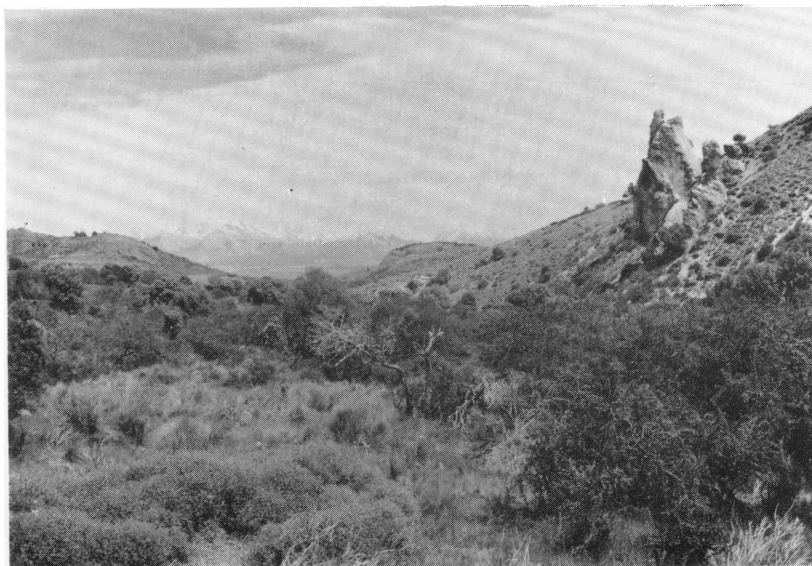


FIG. 18. Scrub woodland in steppes east of San Carlos de Bariloche, Río Negro, Argentina, elevation about 800 m. Habitat of *Colaptes pitius*, which forages on the ground in open areas, but nests in trees and flies into them when alarmed. The Andes Mountains are visible in the background.

molt and aspects of morphology is discussed in the taxonomic section.

Colaptes pitius

I observed the Chilean Flicker in the Andes of south-central Argentina during November, 1967. Its habitat in Neuquen and Río Negro provinces includes openings within the Fuegian *Nothofagus* forests, the edges of such forests, brushy pastures, the edges of tree plantations, riparian woods, and the borders of scrubby woods that finger out from the forests along ravines into the surrounding steppes (fig. 18). In such situations at an elevation of from 2000 to 3000 feet Chilean Flickers were fairly common. Indeed they were generally more common than the Magellanic Woodpecker (*Campephilus magellanicus*) and the Striped Woodpecker (*Picoides lignarius*), the only other woodpeckers found in this region (see Short, 1970a, 1970b).

This flicker forages mainly on the ground, but is not seen far from trees to which it flies when alarmed. No foraging was observed in trees (I exclude from foraging the "displacement" pecking of alarmed birds which had fled to trees). However, F. Vuilleumier has noted (personal commun.) them searching "rather lazily" for

insects in the tops of trees in western Argentina. Individuals foraged on the ground much in the manner of *Colaptes auratus*, hopping about, swiping and poking at the ground, and digging frequently. Progression on the ground was by hopping only—no walking was observed. The stomachs of birds that were collected contained eggs, larvae, pupae, and adult ants; there were no indications of food items other than ants. However, Cekalovic (1969) has recorded these items from the stomach of a female flicker from Chile: a scorpion, six or more ants (at least one *Camponotus* sp.), and 12 larvae of a scarabaeid beetle.

Other competitors among woodpeckers for food resources are nonexistent in the Fuegian forests, for the Magellanic and Striped woodpeckers are strictly arboreal foragers. In this foraging neither of these species consumes ants to a great degree. Even nest-site competition with these woodpeckers is apt to be minimal, for the Magellanic Woodpecker is much larger than the Chilean Flicker, whereas the Striped Woodpecker is much smaller than the latter. Thus, they generally require larger and smaller trees for nesting, respectively, than does the Chilean Flicker (see Short, 1970a). This fact

plus their preference for the interior of forests limits their contact and hence possible competition with the flicker.

The nesting season includes October and November in the region where I studied the Chilean Flicker. A nest was discovered 12 feet up in a dead stub on an island in a creek 8 km. east of San Martín de los Andes, Neuquén, on November 19. The habitat was severely limited riparian vegetation about a tree plantation in open country a mile or so from cutover *Nothofagus* forest. Five young flickers were found in the nest, including one just hatching from an egg. An adult male taken on November 21 at 18 km. north of San Martín de los Andes had a brood patch and testes measuring 15 by 6 mm. with a 9 mm. curved tip (left) and 11 by 7 mm. (right). An adult female taken November 20 at 4 km. north of San Martín de los Andes had a brood patch, and had laid eggs (ovary 10 by 5 mm., oviduct enlarged), whereas its mate had enlarged testes (left 9 by 4 mm. with 5 mm. curved extension, and right 5 by 3 mm.). An adult male, and four adult females taken at several localities up to 26 km. east of San Carlos de Bariloche, Río Negro, on November 26 and 27 showed similar indications of breeding activity. All five of these birds had brood patches, and the females had an ovary 10 mm. or longer in each instance (one female had three burst follicles and ova as large as 7 mm. in diameter).

Information regarding the behavior and vocalizations of this flicker is presented below. Seven breeding adult females collected in late November weighed from 146 to 163 gm. (average 156.6 gm.). Three adult males collected in the same period weighed from 151 to 161 gm. Five young birds in a nest on November 19 weighed 20.3, 19.9, 16.9, 9.6 and 4.9 gm.—the last bird was in the process of hatching at that time (obviously the two small birds would be at a disadvantage if food was scarce). Eye color in adults of this species varies from very pale yellow to lemon-yellow. The color of the legs of Chilean Flickers is gray or greenish gray.

Colaptes rupicola

During late July and August, 1968, I studied in Peru two forms (*cinereicapillus*, *puna*) of the Andean Flicker and birds intermediate between these forms. Additional but casual observations were gained from a third race, *C. r.*

rupicola in Jujuy, Argentina, and in the Bolivian highlands during that same period. Those features of habits and morphology discussed in this section (displays, vocalizations, and molts are discussed below) appeared alike in the races I observed. The Andean Flicker is entirely terrestrial, although birds living in the few highland areas where there are trees readily use them as perches (they use them too for displays and for surveillance). I observed Andean Flickers in the puna between elevations of 2900 and 4950 m. (figs. 7–11), frequently about habitations and broken (rocky, rolling) terrain, and uncommonly in flat, open country.

Rocks, cliffs, buildings, road cuttings, and banks of streams are favorite perches of the Andean Flicker. Before the flickers descend to the ground to feed they pause on one of these perches, and when startled while they are feeding they hop or fly back to such a vantage point before resuming their interrupted activity. If they are only mildly frightened, they may return to the ground below a vantage point and commence foraging briefly, then reappear at the perch in a few moments for another look. Of course their actions vary with the circumstances, but the birds inevitably are wary and difficult to approach. When they are severely startled, they fly far, often over or around a mass of rock out of sight of the intruder. Although Andean Flickers may occur at least for foraging in flat areas of the puna, their preferred habitats are the grassy areas about outcrops, particularly where cliff-faces are present, and broken, rock-studded hill slopes. They also are encountered frequently in and around the small puna villages, perching on adobe buildings and foraging in the fields. Indeed, the disrupted landscape and buildings about villages seem to provide the best available habitat for Andean Flickers in the extensive flat portions of the Peruvian-Bolivian Altiplano.

Foraging is accomplished on the ground. I have observed one Andean Flicker pecking at a branch of a eucalyptus tree in which it was perched in the Peruvian town of Huallanca, but the bird had been disturbed by my approach and appeared not to be foraging. Its pecking may be termed a displacement activity. The flickers normally walk about while foraging on level ground which has no obstructions, but they frequently bound (hopping) up or down steep slopes, in rocky places, and in dense grass.

Foraging is in the typical flicker manner. The very long bill probes and swipes from side to side, flinging away dirt and pebbles as the bird searches for prey. The flickers may dig up to 5 cm. deep into the earth to obtain a larva. Their food (races *puna*, *cinereicapillus*) consists mainly of large "grubs," most of which are lepidopterous larvae, dug from the ground at the bases of grass tussocks. These larvae were not identified, but rather few species seem involved as they were very similar in the several regions where we studied. The larvae often were 2 to 3 cm. long, and up to 29 were counted in the stomach of one bird. In all, 25 stomachs contained these larvae. One stomach contained no lepidopterous larvae, but instead had several coleopterous larvae. The only other items noted were several small seeds and pieces of undetermined small (adult) insects in a stomach, together with eight lepidopterous larvae, and a few small stones in two other stomachs. Ants were rarely seen in the *puna*, and apparently they are not sufficiently common to serve as a major dietary item, or the species present are for some reason not suitable as food for the flickers. One effect of the lack of dependence on ants by the Andean Flicker is that these birds forage more uniformly over the ground than do other flickers, which tend to concentrate their efforts in the vicinity of ant nests. I lack data on the foods of the Andean Flicker at other seasons, and hence it is not known whether its diet varies seasonally.

There is no information to suggest that extensive migrations occur in any of the South American flickers. However, it is possible that Andean Flickers move downslope from higher elevations for the winter, and possibly after breeding for a part of the summer (when snow may occur because of the wet season; see below). On the other hand, nonbreeding birds may move downslope several miles or so to forage, and then return upslope daily. Several flocks of up to 15 birds were encountered on the mornings of August 22 and 23 near Cerro de Pasco, Peru. These birds appeared to be moving in groups, and they disappeared downslope toward that city, which was several miles away and 1200 feet lower in elevation. We were unable to establish whether they returned upslope in the evening. Downslope foraging may account for most occurrences of *rupicola* at elevations below 2800 or 2900 m. in Peru and Bolivia.

It is not known whether other birds such as one of several species of furnariids may compete for food with the Andean Flicker, but competition with other woodpeckers is nonexistent. Rarely the Andean Flicker may descend sufficiently far downslope to come into contact with one or another woodpecker (e.g., *Piculus rivolii* in Peru, or *Picoides lignarius* or *Colaptes melanochloros* in Bolivia) at the upper limit of montane woodland. Such contacts probably do not occur during the breeding season of *rupicola*. Data from specimen labels suggest that the Andean Flicker descends to the lowest elevations in the northern part of its range, where *cinereicapillus* has been taken at 7500 feet (Chachapoyas, Peru, data from specimens in the American Museum of Natural History). *C. r. rupicola* has been observed (Vuilleumier, *in litt.*) in Jujuy, Argentina, as low as 2000 m., where it was not thought to breed.

Observed displays and gonad condition of specimens (see below) suggest that the breeding season commences in September in Central Peru. The breeding schedule probably varies greatly in the Andean Flicker from region to region, and within an area it may vary altitudinally. At higher altitudes in the Andes Mountains close to the equator the seasonal variation in temperature is not great. The late spring and summer (late December to March) rainy season in highland Peru (above an altitude of about 4500 m.) may be critical for these flickers, as the cold rains and frequent snows of that season can cause the collapse of some sites in which nests are excavated, thus posing problems in raising young. Thus, the breeding season probably is "sandwiched" between the mid-winter cold and the heavy rains of summer, and young birds are fledged before the height of the rainy season.

Nests are excavated in banks, road cuts, and cliff faces. The birds nest colonially, with as many as 10 pairs or more sharing the same bank (Dorst, 1956). I left the area prior to the nesting season, but Dorst (1956) has described the nest construction in one such colony. The flickers occasionally may nest in adobe buildings, which often are pock-marked with holes excavated by these birds (Short, 1971d, fig. 11). However, natives of several areas assured me that the birds roosted but did not nest in such cavities. I saw no flickers approach these cavities, although I often spent an hour or more near

buildings containing their cavities. I was told by the local residents that the birds excavate and utilize the holes in buildings as roosting holes during the summer rains. Perhaps the overhung roofs of the buildings offer protection from wash-outs and flooding not provided at many cliff sites. The roosting holes are drilled through the outer surface of the adobe building and then curved to one side. Abandoned buildings may be used by birds digging through to the inside, then roosting under the roof while that lasts. Sixty holes were counted in one long-abandoned building.

Of 16 males and 12 females for which gonadal information was obtained in Central Peru, none was in full breeding condition, although all had somewhat enlarged gonads. The birds were collected between August 9 and August 25. Male left testes varied from 3 mm. by 1 mm. with a curved projection 2 mm. long to 8 mm. by 5 mm. with a curved projection 4 mm. long. The ovary of females varied from 5 mm. by 2 mm. to 11 mm. by 6 mm., and all had small ova (measuring 1 mm. or less in diameter in all but one bird that had ova 2 mm. in diameter). Because the gonads of all these adults were enlarged to some degree, and there were no signs of nesting having occurred just prior to my arrival, it seems likely that the breeding season commences in September and October. Dorst (1956) found nests with young in February, and he suggested that sporadic nesting occurs throughout the year. Immature specimens are available representing the months of January (*puna*—Junin, Peru), February (*rupicola*—Jujuy, Argentina), and March (*puna*—Junin, *cinereicapillus*—Chachapayas, Peru).

Information about the behavior, vocalizations and molt of *rupicola* is presented elsewhere in the present report. Males weighed from 148 gm. to 192 gm. (average 176.5 gm. for 16 males), although the one bird at 148 gm. was 16 gm. lighter than the next heaviest bird. Females weighed from 153 to 183 gm. (average 168.3 gm. for 12 females). These Central Peru birds are variously intermediate between *C. r. puna* and *C. r. cinereicapillus*, with individuals representing phenotypes ascribable to both forms. The bill of the Andean Flicker is black, and its eyes are lemon-yellow (*C. r. puna*, *C. r. cinereicapillus*). The color of the legs varies from dull yellowish green (*puna*) to pale orange-yellow (*cinereicapillus*).

Colaptes campestris

The Campo Flicker (only the southern race *campestris* was observed) was studied sporadically during September to November, 1967, and in September, 1968, in diverse habitats including clearings (fig. 17) in subtropical moist forest (Misiones), "gallery" forest borders (Corrientes, Short, 1971e, fig. 4), pampas (Corrientes, Short, 1971d, fig. 3), pantanal (eastern Formosa), open areas in chaco woodland (Corrientes, Chaco, Formosa; see Short, 1970a, fig. 1), and pampas-steppe ecotone (Río Negro). Although this flicker is a common denizen of open, treeless pampas, it is often abundant where there are some trees (eucalyptus or other plantings and edges of various forests and woodlands). It can accommodate to man's cultivation, as in Misiones where it seems to be following in the wake of the clearing of forests. Given considerable open grassland country for foraging, its abundance may be determined by the availability of nest sites (see below).

Foraging seems entirely terrestrial in the Campo Flicker, for the only arboreal "feeding" that I observed was a form of displacement pecking by birds that had just been flushed from the ground. Arboreal perches, or perches on telephone or fence poles are favored, however, and displays and calls often occur at such sites. The birds hop when moving long distances, or on uneven terrain, such as up (or down) an anthill. When actively feeding, however, they walk about easily. In the vicinity of woods there may be competition between this flicker and the Green-barred Flicker, which seems to derive benefit from foraging mutually at anthills (Short, 1969b). Their food consists mainly, if not entirely, of ants as stomachs of eight specimens contained no food items other than ants, their eggs, larvae, and pupae.

The Campo Flicker is moderately social, although not so much as is the Andean Flicker. During the nesting season, it is more common to see groups of three, or less frequently four birds than single birds or pairs. Favored areas may have a concentration of nesting pairs, but the nests usually are not situated in the same tree or fence post or even in adjacent posts. Up to eight birds have been observed at one time foraging in a small area, and up to six birds at a single anthill. However, within these groups the birds generally associate in pairs or trios. It is possible that small groups represent the parents

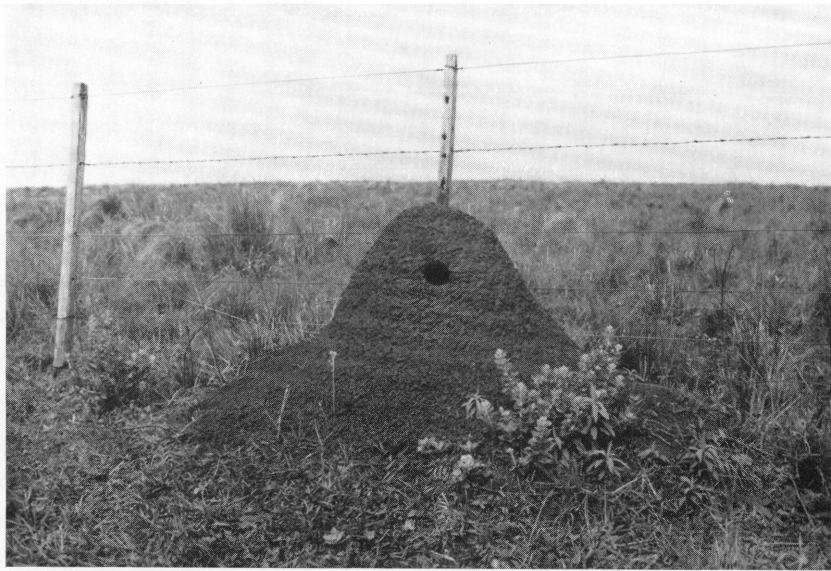


FIG. 19. Nest of *Colaptes campestris campestris* in termite mound, northeastern Corrientes, Argentina. The nest, which contained four eggs on October 1, 1967, was about 12 in. deep at the end of the entrance tunnel, which was 8 in. long. The site is in upland pampas near the Misiones border.

and part of a brood from a previous year, but studies of postbreeding family groups are needed to establish this. It is also possible that trios are comprised of unrelated (not a mated pair or the brood of a previous year) birds of both sexes, a single bird (perhaps usually a male) of one sex and two (perhaps females) birds of the opposite sex, either about equally motivated to reproduce, or very unequally motivated to reproduce (an incipient "helper-at-the-nest" situation). One trio obtained in northeastern Corrientes on September 28 was composed of a male weighing 170 gm. and with enlarged testes (left—13 by 5 mm. with a 7 mm. curved tip, and right—11 by 6 mm.), and two females weighing 167 gm. and 155 gm. The heavier of the two females had a smaller ovary (10 mm. in diameter) and ova (1.5 mm.), whereas the lighter female had a very large ovary (17 mm. in diameter) and ova (to 5.5 mm.).

Breeding activity seems to commence in late August and early September in northern Argentina. Young birds are fledging by early October, which probably marks the height of the breeding season. Nests were observed frequently, and all those that were observed were solitary nests.

No evidence was found for nesting of pairs in very close proximity, although semi-colonial nesting was occasionally noted. In one case four occupied nesting holes were found in 70 yards; this was in a line of old eucalyptus trees, and the nests were as close as every other tree (one instance), but not in adjacent trees or in the same tree. An estimated eight to 10 nesting pairs occupied a 200-yard double line of eucalyptus trees in northeastern Corrientes.

These flickers seem to prefer trees and telegraph poles or large fence posts where available, and their numbers were greatest at such sites. Lacking trees on the open pampas, the birds dig cavities (fig. 19) in larger termite mounds or in banks along roadways. It is well to note that much of northern Argentina is flat, and the level pampas are often extensively flooded after a heavy rain. Thus, this woodpecker appears not to burrow directly into the ground on flat terrain. At the edges of forests nesting sites are selected in dead trees or dead stubs of living trees immediately bordering open pampas or cultivated fields. The birds do not penetrate the woods for more than a few yards, even if apparently suitable trees occur

just within the forest. Nests in trees were observed as high as 40 feet. The birds excavate the cavity in the manner of other woodpeckers. The clutch size seems to be four or five eggs, and family parties most frequently include four young birds.

All nine adults collected in Misiones, Corrientes, and Formosa during late September and October had enlarged gonads. Among three males the smallest testis length was 9 mm., whereas the smallest ovary among four females measured 10 mm. in diameter. All the adult flickers had a fully developed brood patch.

Three adult males weighed from 161 to 192 gm., and four adult females weighed from 145 to 167 gm. (averages are 174 and 158 gm., respectively). In contrast to the pale-eyed Andean and Chilean flickers, the Campo Flicker has dark (chestnut) irides.

Similar data for the northern *Colaptes campestris campestris* are fragmentary or lacking, but I do not expect that form to differ significantly (except of course in seasonality of breeding) in the aspects of biology I have discussed for *campestris*.

INSTRUMENTAL SIGNALS AND VOCALIZATIONS

Many of the vocalizations of South American *Colaptes* were heard and some were recorded during the course of my field studies. These represent a portion of the repertory of each species (*Colaptes pitius* was recorded least). Obviously individual and especially seasonal variation, and geographic variation of the various vocalizations remain to be investigated. Only the barest insight into the nature and possible functions of certain vocalizations can be discussed at this time. Nevertheless these vocalizations provide some comparative data of use in evaluating relationships within the genus. Previously unpublished studies of mine and of Jerome Barry, who worked with me for two summers, of the North American Flicker (*C. auratus*) provide a framework for the discussion. These studies, conducted in the field and in aviaries over parts of 15 years, somewhat enable me to interpret variation among the South American flickers. Some of the terminology has been employed previously (Short 1970a, 1971b), and the framework for a discussion of vocalizations follows that used in Short (1971b).

INSTRUMENTAL SIGNALS

The only instrumental signal known in flickers is drumming, which has been documented so far only for *Colaptes auratus* and *C. melanochloros* (Wetmore, 1926; *C. m. nigroviridis* in Formosa, Argentina). According to Wetmore (1926, p. 222), the drumming of *melanochloros* "suggested the sound produced by *Colaptes auratus*, but was delivered more slowly." I heard drumming possibly by this species only rarely, and but once could I see the bird. In this instance it was a female drumming 15 m. up a tree near Itá-Ibaté, Corrientes, on October 31. The drumming was indeed slow compared with *auratus*, which is interesting in that the Long Call of *melanochloros* also is slower than that of *auratus* (see below). Other species of the green flicker group, especially *C. punctigula*, are apt to drum. However, it is unlikely that the terrestrial *rupicola* and *campestris* drum; *pitius*, which is somewhat more arboreal, is not known to drum.

A sound thought at first to be produced by the wings of *Colaptes auratus* in flight, seems to be a vocalization, and has been termed the Whurgle by J. Barry (unpublished report). As yet no other flicker is known to produce this sound, which will not be discussed further herein.

VOCALIZATIONS

Woodpeckers are considerably vocal, exhibiting a great variety of calls. Interspecific differences can be shown in the case of different calls used in the same, or similar behavioral contexts, and in an instance in which structurally similar calls are employed in different contexts. Only a few such differences can be documented at this time. Obviously further studies of variation, and investigations of the ontogeny of vocalizations are needed before we can treat flicker vocalizations with certitude.

THE PEAH CALL AND POSSIBLE EQUIVALENTS

The Peah Call of *Colaptes auratus* is a relatively long, but variable, usually loud vocalization serving as an alarm call, and possibly as a threat display. The alarm version (fig. 20k) is loud, about 0.20 to 0.45 second in duration, and consists of a note diminishing (often in distinct stages, steplike) in pitch and in volume from an initial 3 to 7 kc. to as low as 1 to 3 kc. The drop in pitch is sometimes great, even as much as 4 kc. and often in two or occasionally in three steps.

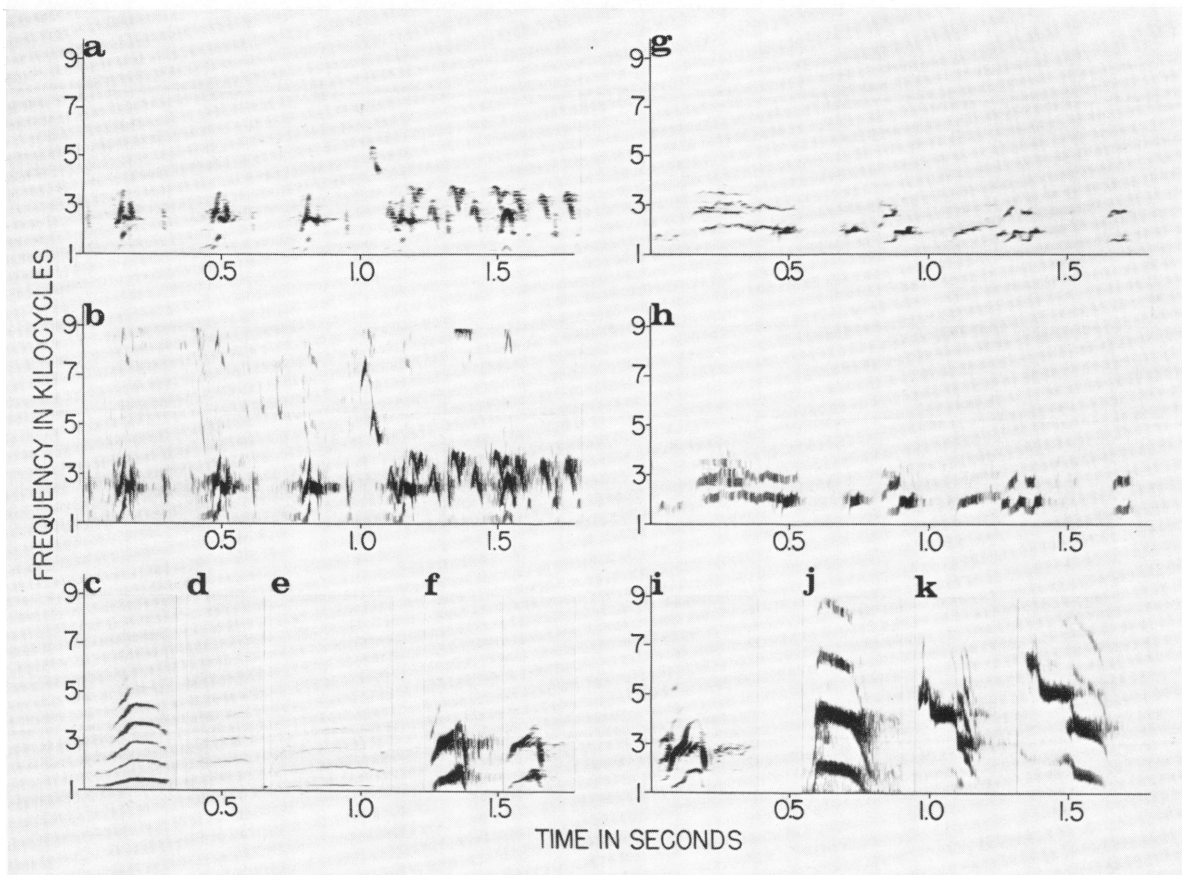


FIG. 20. Sound spectrograms of several species of flickers. a. Wicka Call of *Colaptes melanochloros melanochloros* × *nigroviridis*, both male and female of a pair, NB. b. As (a), but WB. c. Horizontal element of one type of nestling call, *Colaptes auratus luteus*, NB. d. Low note ("chewa") of *Colaptes punctigula*, NB. e. "Peeea" note of *Colaptes rupicola puna*, NB. f. Single element of Quoick Call of *Colaptes rupicola puna*, WB followed by NB. g. Part of low Wicka Call of *Colaptes campestris campestris*, NB. h. As (g), but WB. i. Variant element of Quoick Call of *C. rupicola puna*, NB (compare with f). j. Peah Call of *Colaptes atricollis*, WB. k. Peah Call of *Colaptes auratus luteus*, WB; call of immature bird in nest, then adult female. The sonograms are narrow band (NB) or wide band (WB). Please note that frequencies of c-e, g, h, are 0.5 kc. lower than indicated above.

At times the Peah Call drops only slightly in pitch, say from 4 kc. to 3 kc., with no step. The soft version, which is not illustrated, is a barely audible peah given at times before an attack by a dominant flicker. Captive North American Flickers respond, for example, to a sudden noise, entry into the aviary by a stranger or a nearby dog, with the loud alarm peah, whereas they frequently approach the observer with whom they are familiar with a low peah accompanied by other aggressive signals. Observations in the field confirm these functions, but studies of the soft Peah Call are needed because the note is

inaudible at a distance and hence there is a paucity of observations.

Colaptes atricollis has a somewhat similar call, sounding like "peah" (fig. 20j); six recorded calls were from 0.21 to 0.25 second in duration, and were marked by an abrupt rise (in the strong first harmonic tone from 2 or 2.5 kc. to 4 kc.), followed by a gentle downward tapering, and then a steeper slope which drops to 2 kc. or less (first harmonic). The harmonics of this call are strong, with a fundamental tone peaking at 2 kc. The Peah Call of *atricollis* seems to function as an alarm call, although it may be more

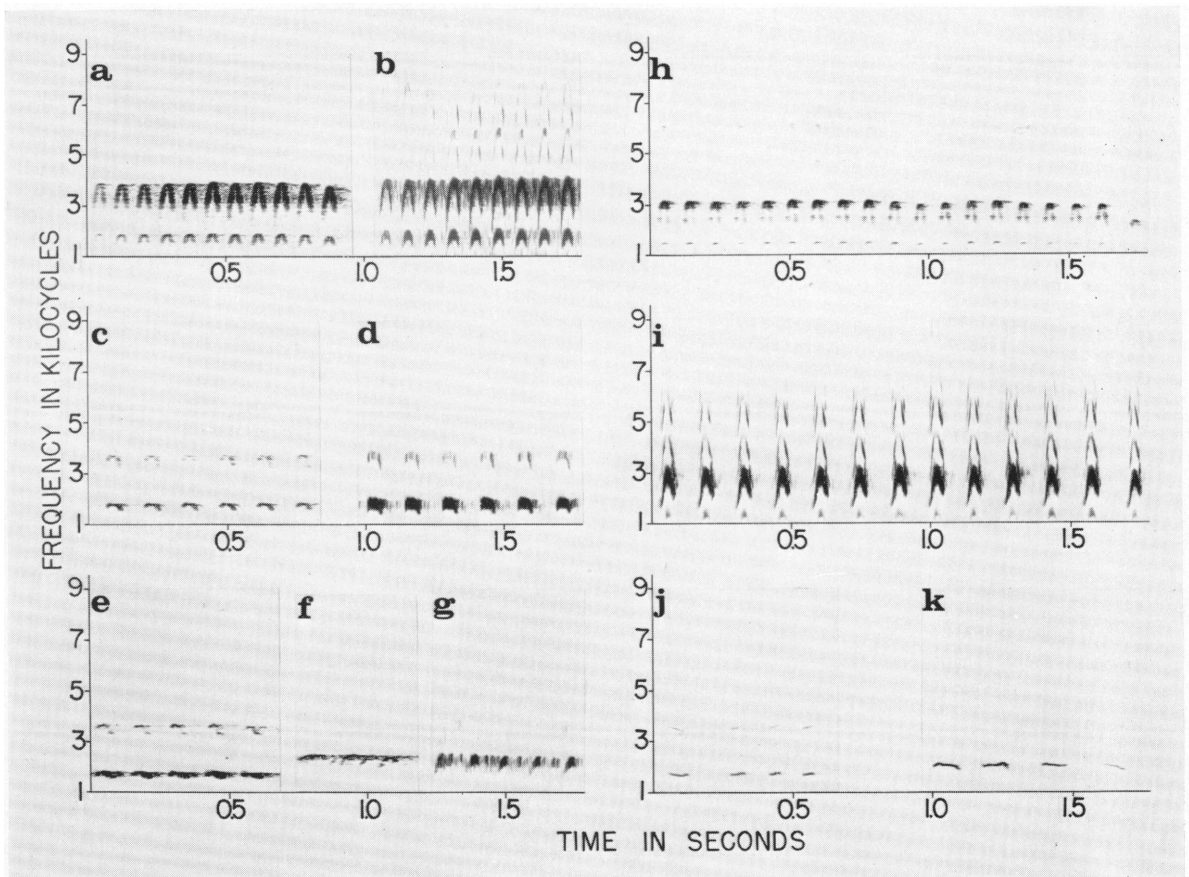


FIG. 21. Sound spectrograms of several species of flickers. a. Full Long Call of *Colaptes atricollis*, NB. b. Initial 9 notes of (a), WB. c. Part of Long Call of *Colaptes punctigula*, NB. d. As (c), WB. e. Part of rapid, variant Long Call of *C. punctigula*, NB. f. Part of Long Call of *Colaptes campestris campestris*, NB. g. Part of same call as (f), WB. h. Terminal part of Long Call of *Colaptes auratus luteus*, NB. i. Middle portion of Long Call of *C. a. luteus*, WB. j. Whistled call of *Colaptes punctigula*, NB. k. Whistled call of *Colaptes rupicola puna*, NB. The sonograms are narrow band (NB) or wide band (WB).

commonly emitted (it was heard frequently) and have other functions as well.

In Formosa, Argentina, I startled a Green-barred Flicker foraging on the ground, and it flew to a tree and uttered a peah note very like that of *auratus*. The call was repeated several times, but I was unable to record it. It appears to be less common than in *auratus*, perhaps because alarmed birds call less frequently; rather they tend to fly rapidly away without calling. Different calls seem to serve the alarm function in other flickers. However, two calls resembling somewhat a peah call were heard from *Colaptes campestris campestris* in Corrientes and in Misiones, Argentina. One call, rendered

"pya" and described as being "not quite as the peah of *auratus*" in my notes, was given by a Campo Flicker flying up from the ground ahead of me, and then perching very close by rather than flying farther away. Another call is given as "kyow" in my notes; it was emitted by a bird upon which I almost stepped before it saw me in thick grass.

WHISTLED CALLS

Whistled notes resembling the three or four note call of the Greater Yellowlegs (*Tringa melanoleuca*) have been described by various authors for *Colaptes pitiús*, *C. campestris*, and *C. rupicola*. These species, as well as *C. punctigula* do

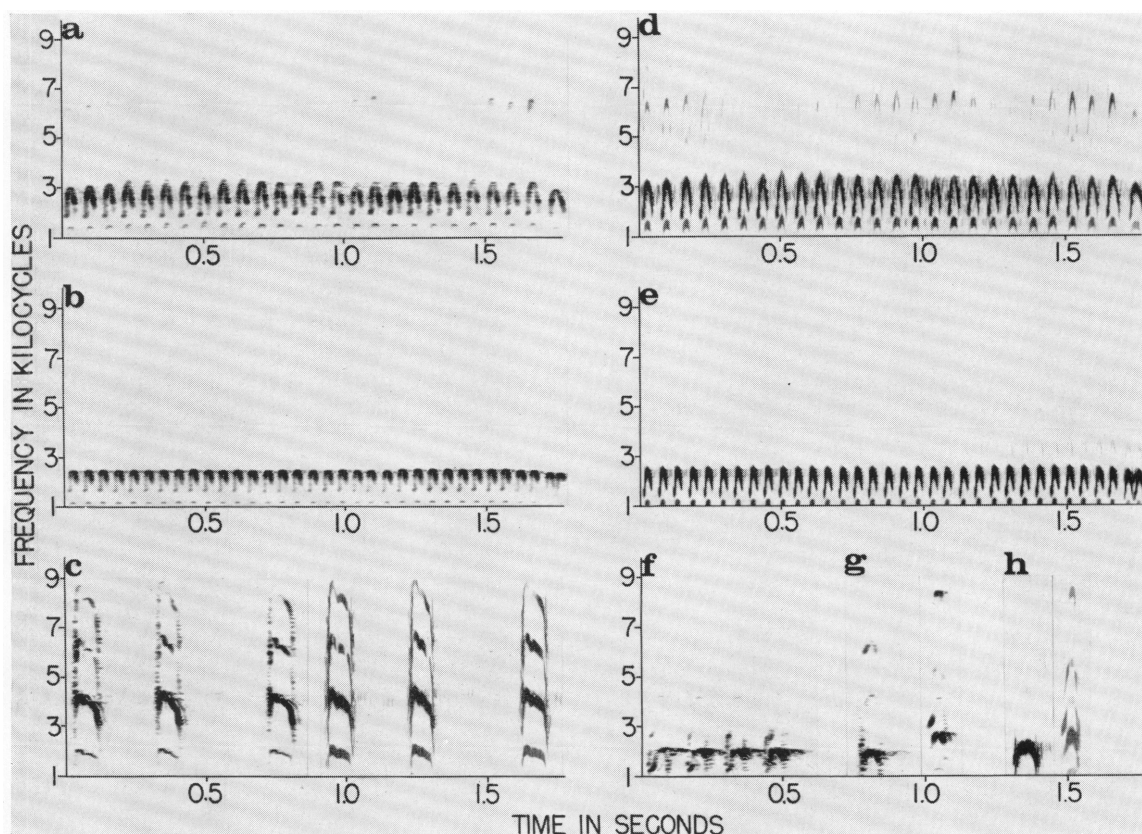


FIG. 22. Sound spectrograms of several species of flickers. a. Terminal part of Long Call of *Colaptes rupicola puna*, NB. b. Terminal part of Long Call of *C. r. cinereicapillus*, NB. c. Three notes of series of Week Calls of *Colaptes campestris campestris*, NB, followed by same notes, WB. d. As (a), WB. e. As (b), WB. f. Series of Peek Calls of *Colaptes rupicola puna*, NB. g. Single Peek Call of *C. r. puna*, followed by that of *C. r. cinereicapillus*, N.B. h. Single Peek Call of *C. r. puna*, followed by that of *C. r. cinereicapillus*, WB. (notes not same as in g.) The sonograms are narrow band (NB) or wide band (WB).

have whistled notes and that of *rupicola* especially resembles the call of the yellowlegs (e.g., compare sonogram on p. 118 of Robbins et al. 1966, with fig. 21k herein). The whistled "tew-tew-tew" of *rupicola* is loud and pure of tone (at about 2 kc.), although slower, and with less change in pitch than the yellowlegs' call. Usually three or four notes comprise a series in *C. rupicola puna*, but single notes may be emitted. This call is uncommon in *C. c. cinereicapillus*, or it was at the time of my studies (less than 100 km. away *puna* was whistling frequently during the same month in which *cinereicapillus* was studied). Only once was such a call heard in *cinereicapillus*, a "Kwee," followed a second or more later by a "kwee-kwee." The calls of *C. r.*

rupicola, which I did not study, seem similar to those of *puna* according to field observations of F. Vuilleumier (*in litt.*) who described them in his field notes as isolated or repetitive "phiu-phiu" or "phiu-thiu-phiu" calls.

I was unable to record the whistles of *piti*, which are given singly or in loose or definite series ("Kwee-Kwee-Kwee"). I found this note to be less loud, longer, and more variable than that of *rupicola*, which it otherwise resembles closely. It may be more similar to that of *campestris* in having stronger harmonics than the call of *rupicola*. This may account for its more "raucous" sound (F. Vuilleumier, *in litt.*, compared this call of *C. piti* and *C. r. rupicola*, stating that the whistles of *rupicola* are "fairly

similar to those of *C. pitius* but less raucous") compared with *rupicola*.

I found that *Colaptes campestris campestroides* uttered whistled notes infrequently, and was unable to obtain tape recordings of one, although I heard a number of distant calls (see Wetmore, 1926, p. 223). This double- or triple-noted call of *C. c. campestris* was recorded in Minas Gerais, Brazil, by W. E. Lanyon. Although other calls interfered with the analysis, the notes of these calls appear to be slightly higher pitched, less intense, longer (0.15 to 0.35 second per note, versus 0.07 to 0.10 second for *C. r. puna*), and with slightly stronger harmonics than those of the whistled calls of *C. r. puna*. Also, the double notes tend to run together rather than being discrete as in *rupicola*. Some of these whistled notes are included in the J. D. Frisch record "O Lendário Paraíso dos Índios" (Som Indústria e Comércio, São Paulo).

The whistled call of *C. punctigula* has stronger harmonics (fig. 21j), and only a single note was heard. This call seemed to follow wick series (see below) occurring during encounters between interacting, paired birds. The call was rendered "whew" in my field notes.

Whistled calls are unknown in other flickers, although studies may show that *melanochloros*, the close relative of *punctigula*, also renders this type of vocalization. Functionally the whistles may serve as location notes, which their quality is well suited for in such open, windy country as is occupied by *rupicola* and *campestris*. Other functions are possible; the whistled note of *punctigula* clearly seems related to agonistic or courtship behavior as it occurs in displaying birds which are engaged in encounters.

THE PEEK OR WEEK CALL

A call sounding like "peek" has been noted in *Colaptes rupicola puna* (fig. 22f-h) and *C. r. cinereicapillus* (fig. 22g, h). A somewhat similar call, the Week Call, is known in *C. c. campestris* (fig. 22c). Such calls otherwise have not been reported in flickers, but they may occur in the green flickers. I heard a male Spot-breasted Flicker call "peek" in a loosely connected series at its nest in Peru, and a male Green-barred Flicker at a nest in Corrientes, Argentina, uttered a "week-week-week." The calls of *rupicola* and *campestris* usually are given in series, also.

The peek elements of *C. r. puna* are inverted

U-shaped notes very like those of the Long Call (see below), but with weaker harmonics and lower pitch. Delivered singly or in series, and often associated with Quiock Calls, the fundamental tone peaks at 1.9 to 2.2 kc. When in series the notes are regularly spaced, and emitted at a rate of eight per second. Series may consist of from three to seven notes, each of which is 0.06 to 0.08 second in duration. Single notes are longer, with a duration of up to 0.1 second. Variant notes show tendencies to waver in the initial rise, giving a step effect, and to have a plateau element at the high point additional to the falling portion of the inverted "U." These variants show similarities with the "ik" element of Quiock Calls.

The Peek Call of *C. r. cinereicapillus* differs somewhat from that of *puna* in that the notes are shorter (peak portion 0.04 to 0.05 second in duration), the bases of the inverted U taper outward (especially initially), and the fundamental is at a lower pitch (1.3 to 1.4 kc.) Although given singly or in series just as in *puna*, the notes in series are irregularly spaced at a rate of 2 to 3 per second. The harmonics are somewhat stronger than in *puna*, with the first harmonic (at 2.6 to 2.8 kc. just over that of the fundamental pitch of the call of *puna*) more intense than the fundamental. The most intense portions of the notes are the peak of the first harmonic, the initial part of the second harmonic, and the peak of the fourth harmonic; the peak of the fundamental tone is by far the most intense portion of the call of *puna*.

Calls of *C. c. campestris* recorded by Lanyon in Minas Gerais, and also to be heard on Frisch's record mentioned above, somewhat resemble the Peek Calls of *C. rupicola*. These calls, rendered "keep" or "week," and called Week Calls, occur as irregular series of notes given at 3 or 4 per second. With very strong harmonics they range from 1 to 9 kc. or more in pitch. A note is from 0.07 to 0.12 second in duration, and it begins with an abrupt rise, peaking and then dropping a half kc., followed by a plateauing and finally an abrupt drop. The initial inverted U portion resembles the narrow inverted U of *C. r. cinereicapillus* especially, and the plateau resembles the plateau element of certain peek notes of *C. r. rupicola*.

The function of these calls, and their relation to whistled calls, to alarm calls in general, and to Wick Calls and Long Calls are uncertain. It is

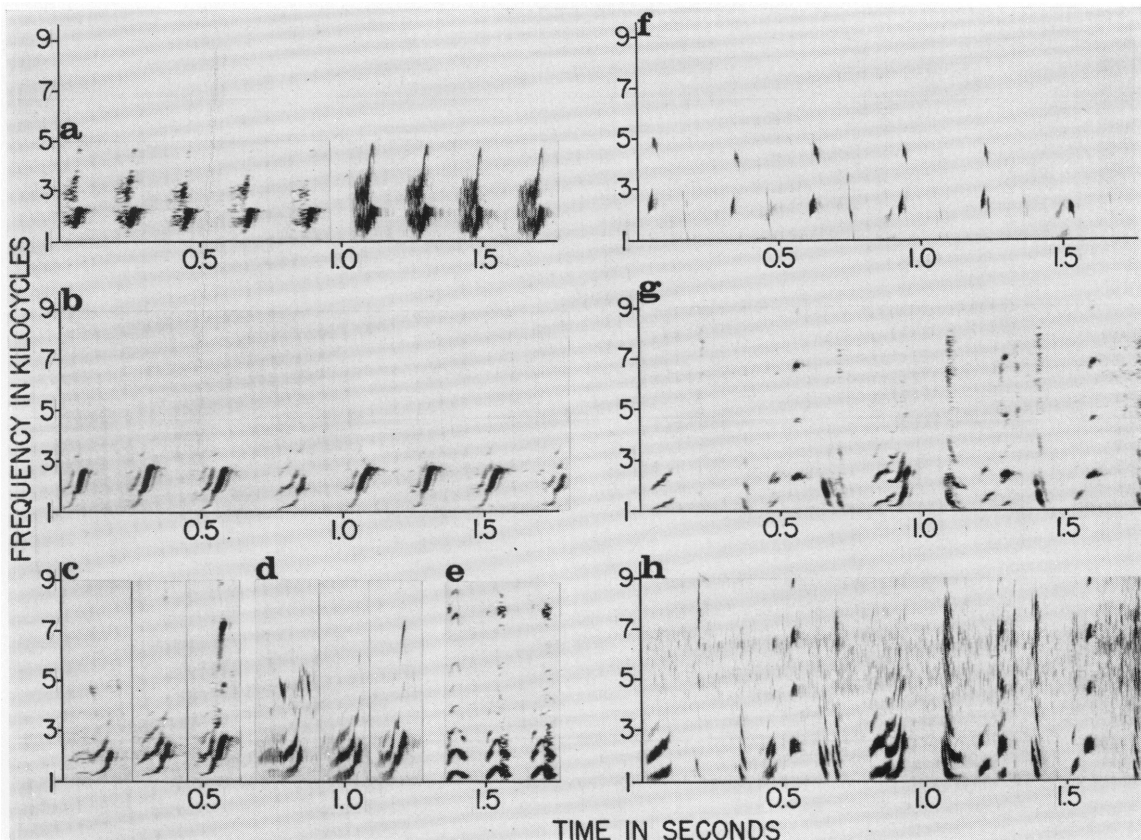


FIG. 23. Sound spectrograms of several species of flickers. a. Part of Wick Call of *Colaptes punctigula*, 5 notes (NB) followed by 4 notes (WB). b. Part of Wick Call of *Colaptes campestris campestris*, NB. Notice variation in the individual notes. c. Three variant notes from Wick Calls of *C. c. campestris*, NB. d. As (c), WB. e. Inverted U-shaped elements of one type of nestling call of *Colaptes auratus luteus*, NB. f. Part of Wicka Call of *C. a. luteus* (New Jersey), WB. g. Part of Wicka Call of *C. a. luteus* (New York), NB. h. As (g), WB. The sonograms are narrow band (NB) or wide band (WB). Please note that the frequency of b-e is 0.5 kc. lower than shown above.

possible that these Peek and Week calls serve as alarm or location calls.

WICKA CALL AND SOME ASSOCIATED NOTES

The Wicka Call is the most complex of flicker calls. Equivalent and indeed structurally similar notes are known for all species except *atricollis*. This call plays a vital role in agonistic and pair formation encounters, with which it is often intimately associated.

Two basic notes most frequently are involved in the Wicka Call (fig. 23f-h) of *Colaptes auratus*. One is an inverted, U-shaped note resembling a weak Long Call note; it is briefer (0.01 to 0.03 second duration) and at a higher pitch

(peak of fundamental tone at 1.9 to 2.5 kc.) than the latter. Frequently this note is alternated in a regular fashion within a given call (although individual Wicka Calls vary considerably *inter se*) with a rising note that varies greatly in all respects. The rising note may rise gradually, or even imperceptibly so as to be essentially horizontal, or it may rise rapidly as a shorter note; an alternate note is a rapidly descending one and invariably brief. Occasionally, when very weak it may be compressed into a rapid vertical note. The fundamental and lower harmonics are strong relative to other harmonics. This note varies from 0.02 to 0.35 second or more in length, depending on its form (shorter

if vertical, longer if horizontal). Shorter notes tend to occur with stronger inverted U notes, longer ones with weaker inverted U notes or in their absence. Wicka Calls may last as long as 4 seconds or more, and individual notes are emitted at intervals of 0.15 to 0.35 second.

Several points are instructive in relating the Wicka Call of *auratus* to similar calls of South American flickers. The Wicka Call of *auratus* may emphasize the rising note variously, such as "cha-WEEK-a, cha-WEEK-a," "chew-EK-a, chew-EK-a," or "WEEK-a, WEEK-a," or it may emphasize the inverted U-shaped note, as "wi-KUP, wi-KUP" or "wi-KA, wi-KA." Long (horizontal) soft rising notes which actually rise little (e.g., some in fig. 23h) may sound like "Kaa-a, Kaa-aa" or "ew-i, ew-i." The rising notes are emphasized, or they are used exclusive of the inverted U notes in low intensity calls occurring during encounters between paired birds, for example, or they are given by an adult as it approaches its nest containing young birds or perhaps its mate. They also frequently are emphasized in long agonistic encounters between evenly matched opponents. In contrast the inverted U-shaped notes are emphasized in Wicka Calls uttered during agonistic encounters, especially initially, or in brief encounters in which they seem to be emitted by the dominant bird. I surmise that the Wicka Call is essentially an agonistic display, that the inverted U notes are elements connoting strong threat behavior, and that the rising notes tend to indicate submissive behavior or a tendency to flee. The familiar buzzy calls of nestling flickers (fig. 23e) structurally are like the inverted U-shaped notes of the Wicka Call, and young flickers also give rising notes (fig. 20c) like those of the Wicka Call; these two notes are rendered completely independently in the young birds. The Wicka Call has equivalents, structurally and functionally, in other woodpeckers as well (Short, 1971b).

I failed to detect this call during brief observations of *C. atricollis*. The functional and to some extent structural homologue of the Wicka Call in *punctigula* is its Wick Call, discussed below. Terminal notes of this call have the form of rising notes of *C. auratus*, and the call itself is employed during agonistic encounters. More *auratus*-like calls of *punctigula* that were heard but not recorded include a "ta-wick, ta-wick, ta-wick" and a "week-a, week-a" accompany-

ing Head Swinging and Head Bobbing between members of a pair meeting at their nest, and very low calls ("pee-ya, pee-ya") uttered by single adults approaching the nest. A low "chewee" note of this type was recorded (fig. 20d); it is a horizontal note resembling calls of juvenile North American Flickers (fig. 20c), and Wicka Calls of *C. campestris campestris* (fig. 20g, h), as well as a low call of *C. rupicola puna* (fig. 20e).

Green-barred Flickers use a Wicka Call indistinguishable to my ear from some such calls of *C. auratus*. One such call (fig. 20a, b), emitted by a male (*C. melanochloros melanochloros* + *nigroviridis*) approaching a female that was perched beside its nest, was rendered "ta-wick, ta-wick." The terminal note of this call, obscured by background noises in the sonogram and hence not figured, is a typical Long Call note very closely resembling the notes of the Long Call of *C. atricollis* (see below); it perhaps was the initiation of an abortive Long Call. The remainder of the Wicka Call is comprised of very short (0.01 to 0.02 second) almost vertical notes which show an inverted U shape under wide band analysis, alternated with a longer, complex element appearing like a combination of an inverted U note and a rising note. The longer note is about 0.10 second in duration with the fundamental and first harmonic (between 1.0 and 3.2 kc.) much the most intense part of it. The three-second long call contained eight double notes, with a slowdown in tempo from a rate of four notes per second to three notes per second. Although no Wicka Call of *C. auratus* is exactly like this call of *melanochloros*, the call of a male North American Flicker recorded by J. Barry at 8:05 AM on June 16, 1969, at Kalbfleisch Research Station, Huntington, New York, closely resembles it. Unfortunately the *auratus* call is too low in intensity and the background noise is too great for all its details to be apparent in a sonogram. Other Wicka Calls of *C. melanochloros* heard but not recorded varied considerably; usually they seemed sharper than those of *auratus*, but this may reflect the particular circumstances of the instances in which they were heard.

Only one Wicka Call, a "week-a, week-a, week-a," was heard from *C. pitius* in an encounter between a male and a female. The call which was not recorded, seemed higher-pitched than that of *auratus* but quite similar generally.

Low Wicka Calls were heard on a number of occasions from *Colaptes campestris campestris*, which also utilizes a Wick Call (see below). These low calls, rendered in my notes as "we-a, we-a" and "Kwih, Kya-wi, Kya-wi," have the quality of the low Wicka Calls of *auratus*. The few calls that were recorded (fig. 20g, h) are long and resemble the more horizontal rising notes of calls of *C. auratus*. The initial notes of the Wick Call of *campestris* are similar (fig. 23b-d). These notes, which sound like "waa-waa," "chew-aaa," or even "Ka-Ka-a-a-Ka-waah," are variable rising notes, although some are nearly horizontal. They last for up to 0.2 second, and a series of several notes over 0.3 to 0.4 second may introduce a Wick Call.

Wicka Calls similar to those of *campestris* are not common in *C. rupicola puna*, and I heard but one (a "Kwa-Kwa-Kwa") from *C. r. cinereicapillus*. Dorst (1956) described such calls as loud and nasal (ou-é, ou-é), and accompanying head raising and head lowering of displaying birds facing one another in southern Peru (*C. r. puna*), and I have heard "wee-a, wee-a" calls from Andean Flickers perched close together (fig. 20e); these appear like horizontal Wicka Call notes of other flickers, as noted above. Generally, interactions were not observed frequently at the season in which I studied the birds, which used Quoick Calls and Peek Calls when they were in proximity to one another.

Elements of a Wicka Call are present in the repertory of all flickers except *atricollis*, in which it probably also occurs. The terrestrial flickers *campestris* and *rupicola*, and *punctigula*, and perhaps others employ Wick Calls (or Quoick Calls) in place of Wicka Calls to some extent, or have other calls that supplement Wicka Calls.

QUOICK CALL

A single note or well-spaced series of notes sounding like "quoick" (fig. 20f, i) or "cloit" is known only in *Colaptes rupicola puna*, in which it is an important vocalization. The note is complex with strong overtones and an occasional second element. The notes are 0.15 to 0.25 second in duration, rising, then wavering, then rising, and finally falling off rapidly. The second element when it occurs rises, plateaus, and then either drops off or continues past the termination of the other element. Longer versions, rendered "quoi-ik" or even "quoi-ik-ik" repeat only the second element once or twice;

the note then lasts as long as 0.5 second. Although a Wick Call is not known in *rupicola*, the Quoick Call notes structurally bear resemblance to the notes of the Wick Call of *campestris*. The main element of the Quoick Call seems like the rising note of the Wicka Call as well. The Quoick Call seems to be given when two birds come into contact. Although Quoick Calls often are interspersed with Peek Calls, the latter are emitted more generally and seem more likely to be location calls, whereas Quoick Calls perhaps have a more aggressive connotation.

THE WICK CALL

The last of the elements and calls that seem related directly to the Wicka Call is the Wick Call, a series of notes so far known to occur in *C. punctigula*, and *C. campestris*. In both species it appears partly to have replaced the Wicka Call in functioning as an agonistic and perhaps also a pair-maintenance call.

The Spot-breasted Flicker emits the Wick Call (fig. 23a) during Head Swinging and other displays when engaged in an encounter, and sometimes in response to a Long Call. The notes are expressed in series of six to 10 (seven calls), uttered at rates of 5.5 to 6.4 (average 5.97) per second. Each note consists of a variable, generally vertical lead component, followed by a rising note, which may be an inverted U-shaped note with the strong accent on the initial rise. Notes have a very strong first harmonic, and they are about 0.07 second in duration. The first note of a series often has an additional rising and falling element ("Ka-wick" rather than "wick"). The final notes are variable and tend to resemble the rising notes of a Wicka Call of *auratus* and *melanochloros*, the Quoick Call of *rupicola*, and the variant Wick Call notes of *campestris*.

The Wick Call of *Colaptes campestris campestris* is a slow (five notes per second) series of four to 12 or more notes lasting up to 2.65 seconds (fig. 23b-d). The notes are about 0.1 second in duration emitted in regular cadence at about 0.2 second intervals, and their harmonics are strong. The upward rising notes waver, forming in some cases a definite step, then rise sharply to a peak before falling off sharply. The first two or three notes and occasional variant notes elsewhere in the call are longer (0.14 to 0.17 second), flatter, and these rising notes resemble closely those of the Wicka

TABLE 21
SUMMARY OF LONG CALLS OF FLICKERS^a

Form	Notes per second	Pitch in kc. of peak of fundamental tone	Most intense tone	Clarity of notes	N
<i>atricollis</i>	12-13	1.8	Harmonic 1	Good	2 (10)
<i>punctigula</i>	8- 9	1.8	Fundamental	Poor	4 (35)
<i>melanochloros</i>	10?	1.3?	?	Good	(7)
<i>auratus</i>	7-11	1.2-1.9	Harmonic 1	Good	40 (100+)
<i>pitiis</i>	10-12	?	?	Fair	(8)
<i>campestris</i>	8-10	1.8-2.3	Fundamental	Fair	4 (7)
<i>campestroides</i>	9-10	2.0-2.3	Fundamental	Fair	8 (26+)
<i>puna</i>	14-19	1.4-1.6	Harmonic 1	Good	7 (20+)
<i>cinereicapillus</i>	19-20	1.1-1.2	Harmonic 1	Good	15 (30+)

^a Calls given at diverse seasons of year. Data do not include the structurally somewhat different Short Long Calls. N, sample size from sonogram samples, or, in parentheses, samples partly recorded, recorded or heard but not recorded.

Call. The typical notes with reduction of harmonics, emphasis on the upper portion, and speed-up of delivery, would resemble typical Long Call notes. The Wick Call of *C. c. campestris* is similar to that of *campestroides*, except perhaps for a tendency to be lower in pitch.

The Wick Calls clearly seem related to Wicka Calls, although perhaps serving other social functions than those of agonistic or even agonistic-reproductive displays.

LONG CALL

All flickers and many other woodpeckers (e.g., *Picoides*, *Dryocopus*, *Celeus*, *Picus*, and others; Short, 1970a, 1971b, personal observ.) have Long Calls, rattles, or some such vocalization serving generally as a song, that is, in territorial proclamation, attraction of mates, and in other ways. Of course their function may differ in details from species to species.

The Long Call contains a variable number of inverted U-shaped notes. Calls with 40 to 60 notes have been heard from *auratus* and *campestris*. The Long Calls of *atricollis*, *punctigula*, *melanochloros*, and *C. r. rupicola puna* tend to be shorter, whereas *C. r. cinereicapillus*, although variable, has the Long Calls containing the greatest number of notes (up to 66 per call). The calls vary in the tempo of the notes, in the tone which is most intense, in the clarity of individual notes, and in the pitch of the notes. This variation is summarized in table 21.

The calls of *C. atricollis* (fig. 21a, b), *C. melanochloros*, and *C. auratus* (fig. 21h, i), and to a lesser extent of *C. pitiis* are very similar in form and delivery. The other flickers have more mechanical sounding, either slow (*punctigula*, *campestris*) or rapid (*rupicola*) calls.

The Long Call notes of *atricollis* are intense for over 1 kc. (fig. 21a, b) near their peak, and the notes are 0.04 to 0.06 second in duration. A male rendered 10 calls in 45 minutes during August in west central Peru. The Long Call of *punctigula* (fig. 21c-e) contains slightly longer notes (0.05 to 0.08 second in duration), and they are intense only at the peak of the note within a range of 0.1 to 0.2 kc. The call is hence more rattle-like, that is, mechanical in sound. No Long Call of *melanochloros* was recorded, but those heard sounded like the clear calls of *C. auratus*, and a single note identical to a Long Call note, perhaps the beginning of an abortive Long Call was recorded. This note resembles that of *auratus* or *atricollis* in form. The notes of calls of *auratus* resemble those of *atricollis*, although they tend to be more intense late in the note and less intense initially; they are of the same duration. *Colaptes pitiis* has a Long Call similar to that of *auratus*, but tending to be higher in pitch and with less clear notes (personal observ., few recordings available, none good). The Campo Flicker has a variable Long Call (fig. 21f, g) with weak harmonics, and notes receiving great emphasis only in their

TABLE 22
SUMMARY OF VOCALIZATIONS FOUND IN FLICKERS

Form	Peah Call	Whistled Call	Peek (Week) Call	Wicka Call Equivalents				Long Call
				Inverted U Element	Rising element	Quoick Call	Wick Call	
<i>atricollis</i>	+	—	—	?	?	—	—	+
<i>punctigula</i>	—	+	?	?	(+)	—	+	+
<i>melanochloros</i>	+	—	?	+	+	—	—	+
<i>auratus</i>	+	0	0	+	+	0	0	+
<i>pitius</i>	—	+	—	—	?	—	—	+
<i>campestris</i>	?	+	+	—	(+)	—	+	+
<i>campestroides</i>	?	+	?	—	+	—	+	+
<i>puna</i>	—	+	+	—	—	+	?	+
<i>cinereicapillus</i>	—	(+)	+	—	—	?	?	+

Symbols: +, definitely present, although not always structurally identical; ?, possibly occurs in some form; parentheses around +, similar but not identical notes are known; —, unknown; 0, lacking. This list is not meant to be exclusive, as other calls undoubtedly remain to be described.

initial portion within a narrow range (often 0.2 kc.) in pitch. The race *campestris* is like *campestroides* in its Long Call except for a tendency toward more vertical emphasis in the initial part of the component notes. The notes are 0.03 to 0.05 or even 0.08 second in duration.

The Long Call of *Colaptes rupicola puna* differs structurally from that of *C. r. cinereicapillus*. Many Long Calls of the latter were heard (fig. 22b, e), and they showed remarkably little variation except in their overall number of component notes. The Long Call of *cinereicapillus* is uttered at a rate of 19 to 20 notes per second, by far the most rapid call of all flickers. Notes are very much alike with their duration varying within 0.03 to 0.045 second. The notes are intense over a rather large range in pitch. There is a tendency for them to be paired toward the end of a call, a tendency noted also in the rapid Rattle Call of *Picoides nuttallii* (Short, 1971b). The call is rendered "brrrrridip" in my field notes. Fifteen recorded calls varied from 17 to 66 notes per call (average 39). Responses to initiators of calling bouts usually contained fewer notes call for call. The Long Call of *puna* is shorter (seven calls averaged 30 notes per call) and more variable (fig. 22a, d). Usually it is slower; the average rate of delivery was 15.3 notes per second (most calls were at 14 to 15 notes per second, and one at 19 notes per second was exceptional among those that I heard). The notes vary from 0.04 to 0.07 second in duration even within a

call, and the pitch of the intense peaks is variable. Generally they are higher pitched than are notes of *cinereicapillus*. The form of the notes is otherwise similar.

Short Long Calls are known in *auratus* and *campestris*, and they probably occur in other flickers. These are bursts of three to six Long Call notes usually emitted at a slower rate than the longer versions. They probably differ in function, for they seem to occur in association with displays, or in rapidly changing situations. The Long Calls are given from perches at varying intervals, and function probably in several ways noted above. The Long Calls of *auratus* and the other more slowly calling species can be rather well matched by a whistle. Such a whistled Long Call by an observer often elicits responses ranging from Long Calls and drumming in *auratus*, to Week Calls and a Wicka Call in *punctigula* (one instance).

SUMMARY

Table 22

It is clear from the above discussion that much remains to be learned about flicker vocalizations. I will attempt a preliminary comparison based on what is known at present. It is also evident that the North American Flicker shares with the green flickers drumming, a distinct Peah Call, and inverted U elements of Wicka Calls. Special calls or modifications of calls are pronounced in the terrestrial flickers (*campestris*,

rupicola); the calls include a loud whistle, a loud Peek Call, a Quiock Call, and a Wick Call. Some of the differences (table 22) in the last group reflect terrestrial adaptations including shifts to calls more effective in open country, as well as replacement of drumming, which is not possible in open terrain. *Colaptes punctigula* surprisingly shows tendencies toward terrestrial flickers in having a whistled call and a Wick Call. Among the more terrestrial South American flickers, *pitiús* seems least specialized and more like the green flickers and *auratus* in vocalizations. Within the green flicker group *atricollis* is insufficiently known, *melanochloros* seems very like *auratus*, and *punctigula* tends somewhat toward the ground flickers (*campestris*, *rupicola*, *pitiús*). Data are not available for comparing *melanochloros* and *melanolaimus* groups of *C. melanochloros*. It appears that the *campestris* and *campestroides* groups of *C. campestris*, and *puna* and *cinereicapillus* of *C. rupicola* show dissimilarity in the structure of some of their vocalizations; they may have certain different vocalizations or at least they may employ some vocalizations differently as well. In the differences in vocalizations that can be analyzed, *campestris* and *campestroides* are more alike than are *puna* and *cinereicapillus*.

VISUAL DISPLAYS

Visual displays involved chiefly in agonistic encounters, or as alarm signals are common in woodpeckers. As in many species of birds the displays tend to involve the bill and the head, those parts of the bird most proximal to an opponent. Observations of the displays of South American flickers were scattered and sporadic, and they covered only limited parts of one or at most two seasons. Hence, most of the meager data are descriptive or relate directly to comparisons with *Colaptes auratus*, whose displays are very well known to me through many partial seasons of field studies and through studies of birds maintained in captivity for more than four years. I include all known displays of *C. auratus* both for completeness and to encourage the filling in of gaps in our knowledge of the displays of the other flickers.

BILL POKING

This action is perhaps not precisely a display, but a simple low intensity attack usually with supplanting among birds whose dominance

hierarchy is well established. Caged North American Flickers employ bill poking, which is a simple peck usually at the back or side of a bird that usually turns away to avoid being pecked in the head, when supplanting at the feeding dish or in usurping a perch from a cage-mate. I have also seen bill poking among pairs of *Colaptes campestris* feeding very close together at an ant mound; one bird, usually the male, pecks the other and supplants it at a foraging site. Most frequently the blow never lands, as the submissive bird dodges out of the way of the bill of the aggressor. Thus, the movement to peck is effectively a threat display.

BILL DIRECTING

This is a frequently observed threat display, although it is so simple in form (fig. 24) and occurs so rapidly that one must be watchful in order to observe it. Bill Directing is the pointing of the bill at an opponent, usually with the bill held slightly above the horizontal, and often accompanied by a slight forward inclination of the head and body. In caged North American Flickers Bill Directing is employed as a threat display to turn aside an advancing bird which is encroaching upon the "individual distance" limit of another bird. It is used to thwart supplanting at the feeding dish as well. I have observed Bill Directing in *Colaptes punctigula*; a male directed its bill at its mate in supplanting her at the entrance to their nest cavity. I have noted Bill Directing in a pair of Campo Flickers perched in a tree; when one approached the other very closely, the second bird pointed its bill at the first, which paused and then turned aside. Foraging Andean Flickers may Bill Direct in warning an adjacent bird as it is about to cross its path. I saw no differences in the form of the display. From the front this display presents the bill against a background emphasizing the color of the crown, the throat, and the upper breast. These areas tend to be colored in distinctive patterns.

HEAD SWINGING

A conspicuous display in agonistic encounters between flickers is a ritualized side-to-side swinging of the head and of course the bill (fig. 24); the body also may move somewhat. This display, which is common in woodpeckers (Short, 1971b), permits a wide range of tend-

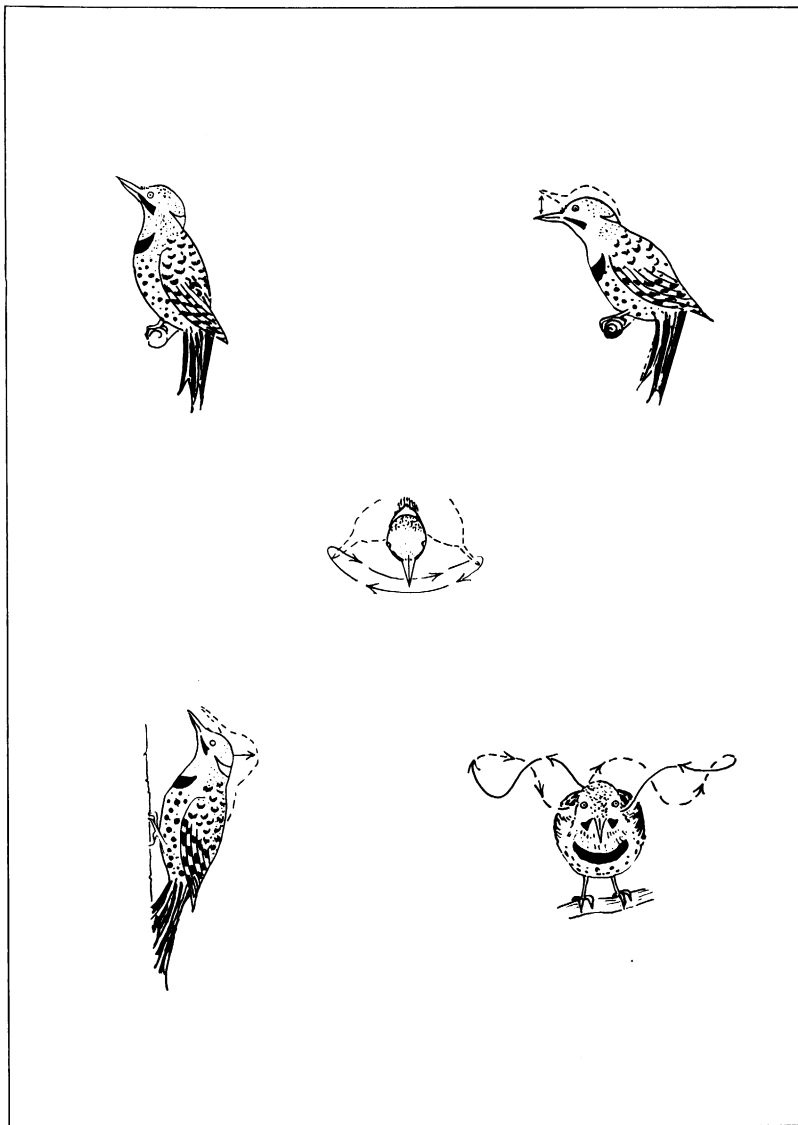


FIG. 24. Some displays of *Colaptes auratus*. Upper left, alarm posture on perch. Lower left, head raising to alarm posture on trunk of tree. Upper right, Bill Directing from head raised (dashed lines) posture. Center, Head Swinging as seen from above. Lower right, combination of Head Swinging (side-to-side) and Head Bobbing (up-down) displays, seen from the front (note emphasis given facial and throat markings). (See text).

encies to be expressed. Essentially the forward aspect of the display emphasizes the bill and hence threat, whereas lateral and upward aspects emphasize withdrawal of the bill and hence a tendency to flee. Encounters between evenly matched opponents are characterized by wide

head swinging. Brief interactions often involve slight, forward directed head swinging—almost Bill Directing—by the dominant bird.

Several instances of Head Swinging were noted in *Colaptes punctigula*. An apparent pair engaged in post-copulatory Head Swinging, with

the head held very high and accompanied by a low call ("week-week-week"). On another occasion a male and a female both indulged in wide Head Swinging accompanied by a low "week-a, week-a, week-a"; the male then Bill Directed at the female and supplanted her. Another encounter featured a brief Head Swing with the head held far above the horizontal, Tail Spreading (see below) and a "ta-wick, ta-wick" call. On August 15 two males were near a female; the males gave Long Calls, then Wick Calls together as they performed rapid Head Swinging and Head Bobbing (see below). Low Wicka Calls also were heard from these males.

Head Swinging was noted only briefly on two occasions in *C. melanochloros*. One bird engaged in a weak Head Swinging Display in front of its mate at their nest. No vocalization was heard. Another double head-swing occurred as a male perched beside its nest entrance while the female was inside; the male emitted a Wicka Call as it waved its head back and forth. Only a few cases were noted in *C. pitius* as well. A female Chilean Flicker calling "pi-cwee, pi-cwee" flew to a dead tree where a male was perched; as the female landed both spread their tails and gave three or four swings of the head far to each side. On another occasion I came upon two adults (sex unknown) calling "week-a, week-a" and Head Swinging far to the sides. Incipient Head Swinging was commonly seen in Andean Flickers when two birds approached very closely; the birds simultaneously swing their heads halfway to either side. More intense Head Swinging accompanied by Head Bobbing was seen in *Colaptes rupicola cinereicapillus*. In one instance a male used Head Swinging and Head Bobbing in front of a female which half faced away, but maintained her tail spread. On another occasion both birds engaged in Head Swinging but only the male gave one or two bobs.

Only weak Head Swinging was seen in Campo Flickers which employ wing movements to a great extent. One male (*campestroides*) gave a Wick Call as it perched before two females Head Swinging slightly. Another male swung its head weakly back and forth several times as it called "K-wi, K-wi" and wing flicked at a female perched nearby. Head Swinging preceded copulation by a male in front of two onlooking adults (sex unknown); the assumed female was quiet and did not give a detectable display as copulation occurred.

This display seems to be prevalent throughout the genus, although its function may vary somewhat.

HEAD BOBBING

The up-down or down-up bobbing of the head (fig. 24), another bill and head posturing display, usually accompanies Head Swinging (fig. 24) in *Colaptes auratus*, although it is much less frequent than is Head Swinging. In concert with Head Swinging the Head Bobbing adds a wavering up-down motion to the side-to-side swinging. As in Head Swinging the forward aspect is interpreted as an emphasis on threat and the upward and downward withdrawal of the bill as an escape or submissive tendency. The addition of Head Bobbing to Head Swinging added to the nuances that can be expressed; bobs with the head in the center of the swing may connote more aggressive tendency and bobs laterally may indicate a greater tendency to flee. Head Bobbing may have evolved from the head up (and sometimes to the side) movement of an alarmed flicker (fig. 24) through ritualization.

Head Bobbing was observed rarely in flickers other than *C. auratus*. Weak or abortive head bobs were seen in *C. melanochloros* and in *C. pitius*. Head Bobbing is frequent in *C. rupicola*, but it is less ritualized than in *C. auratus* and it occurs with and without Head Swinging. In *C. r. puna* a pair seemed to be engaged in disjointed, sporadic bobbing of the head, first to one side and up, and after a pause, to the other side and up. Dorst (1956) described mutual displaying of pairs of this form involving head raising and lowering while the birds were facing each other, accompanied by cries of "ou-é---ou-é." The visual display may have been Head Bobbing or a combination of Head Bobbing and Head Swinging.

TAIL SPREADING

The spreading of the tail accompanies Head Swinging displays when the latter are intense in *Colaptes auratus*. In its extreme form the display consists of the thrusting forward toward the antagonist of the under side of the spread tail as the Head Swinging reaches its lateral extremes, very much as in Tail Spreading of *Picoides* (Short, 1971b, fig. 20). Tail Spreading is most evident during long-lasting encounters between evenly

matched antagonists, and in opponents in clashes occurring when a member of the opposite sex is present during the onset of the breeding season.

Among South American flickers Tail Spreading was noted rarely in *Colaptes melanochloros* and *C. pitius*, and it was seen somewhat frequently in *C. punctigula* and *C. rupicola*.

The tails of two displaying (Head Swinging) members of a pair of Green-barred Flickers were partly spread, especially in the female. The tails of a displaying pair of Chilean Flickers were spread somewhat during one of their Head Swinging Displays. I noticed that a pair of Spot-breasted Flickers maintained their tails in a partly spread condition much of the time when they were together. Their tails were extended more when they overtly engaged in other displays, such as Head Swinging. I noted spread tails among interacting individuals of *Colaptes rupicola puna* several times, and even more frequently spread were the tails of displaying birds of *C. r. cinereicapillus*.

Green flickers have more yellow in the tail than do the ground flickers, and the North American Flicker has the majority of the underside of its tail colored bright yellow or orange. Among the largely black-tailed ground flickers, *C. rupicola* and particularly *C. r. cinereicapillus* have the most yellow visible in the shafts of the rectrices. There appears to be a degree of correlation between the employment of the tail in displays and the brightness of the tail. At present only *C. auratus* is known to do more than spread the tail and that is to direct the tail toward its antagonist. There may be functional differences among the flickers in Tail Spreading.

WING FLICKING AND WING SPREADING

A display involving a rapid, usually partial flicking out, then in again of the wings is observed in aggressive North American Flickers. This display is similar to the simple flight intention wing flicks commonly seen in birds of many species when they are preparing to fly. In the case of the North American Flicker the movement of the wings out from the body displays the yellow (or orange) underwing color to an antagonist. Wing Flicking Displays rarely become full Wing Spreading Displays, with wings fully extended and held in that position, and they are not so ritualized as Wing Spreading in

Picoides (Short, 1971b). Wing Flicking birds may emit a Wicka Call, or they may Gape (see below) and proceed to attack or supplant an antagonist.

Wing Flicking displays probably occur in all species of *Colaptes*, but they undoubtedly vary in function. I saw no Wing Flicking in *atricollis* and none during displays of *punctigula*. A male *melanochloros* did partly spread its wings after landing near a female, which it then supplanted. Wetmore noted (1926, p. 222) that Green-barred Flickers during the breeding season "when calling from a perch had the habit of opening and closing the wings suddenly, to flash the vivid yellow concealed beneath." No Wing Flicking was noted in *pitius*. Both forms of *C. rupicola* that I observed were prone to wing flick lightly when disturbed, as for example after they were flushed from the ground and had retreated to a rock face. Wing Flicking is most fully developed in the Campo Flicker. In this species one wing frequently is flicked while foraging, or whenever a bird assumes a watchful pose. At the slightest alarm a wing is flicked every few seconds (see Short, 1971d, fig. 7). During encounters, the wings are flicked and spread fully, then rapidly drawn in while the bird engages in other displays and emits calls. Wetmore (1926, p. 223) has described a situation involving a group of several Campo Flickers displaying on a post or tree as follows: "they go through many gesticulations with nodding heads, the whole accompanied by loud ejaculations of *whick, whick, whick*. Often one or both wings are extended and retracted quickly with a sudden flash of yellow, as the undersurface of the flight feathers is displayed." It is unknown whether this Wing Spreading is wholly a threat display, or whether it functions in pair formation as well. Possibly it replaces Tail Spreading to some extent in species such as *campestris*, which has little yellow in its tail.

GAPING

This threat display precedes a supplanting attack or bill poking in *Colaptes auratus*. The bill is held momentarily open, and the aggressor then closes the bill and lunges forward at its opponent if it has not given way. It is known otherwise in flickers only in *C. punctigula* in which a male drove away an antagonist, using Gaping as it chased the other male.

TABLE 23

SUMMARY OF THE OCCURRENCE OF VISUAL DISPLAYS IN *Colaptes*^a

Display	<i>atricollis</i>	<i>punctigula</i>	<i>melanochloros</i>	<i>auratus</i>	<i>pitius</i>	<i>campestris</i>	<i>rupicola</i>
Bill Poking	0	0	0	+	0	+	0
Bill Directing	0	+	0	+	0	+	+
Head Swinging	0	+	+	+	+	(+)	+
Head Bobbing	0	0	(+)	+	(+)	0	+
Tail Spreading	0	+	(+)	+	(+)	0	+
Wing Flicking	0	0	+	+	0	++	+
Gaping	0	+	0	+	0	0	0

^a See text for descriptions of displays. Parentheses indicate probable occurrence although perhaps in modified form, ++ denotes expanded, modified form. "0" indicates that the display is so far unknown in that species.

SUMMARY

Table 23

Although we have far from complete information on the occurrence, form, and function of the visual displays, observations suggest that the flickers are relatively uniform in their agonistic displays. Variation in form certainly is not very great in those displays and for those species in which they are known. Minor although distinct differences appear to occur in the form of Tail Spreading and Wing Flicking and Spreading, and perhaps Head Bobbing. Some of these differences appear related to the adoption of terrestrial habits by the ground flickers.

PAIR FORMATION AND POSSIBLE ISOLATING MECHANISMS

I have noted elsewhere (Short, 1971b) the predominance of agnostic behavior in the social life of woodpeckers, and the primary importance of sexual recognition occurring throughout the year in woodpeckers. These factors result in pair formation through the employment of sexual recognition characters in repeated agonistic encounters between a prospective pair. Noble's (1936) experiments with *Colaptes auratus* showed that even the familiarity enjoyed by a mated pair is insufficient to counter the primacy of sexual recognition marks, for a female with her color pattern changed to that of a male was mercilessly attacked by her mate as if she were an alien male. It follows that sexual markings may be especially useful isolating mechanisms in woodpeckers. It is likely also that major differences in vocalizations and visual agonistic displays may serve as reproductive isolating

mechanisms, that is, they might cause disruption of the delicate interaction that must occur if pair formation is to result from intersexual agonistic encounters. Any misunderstanding of the male's displays by a female (or vice versa) may nullify her advantage in lacking male sexual markings, causing her prospective mate either to over-react and attack, or to become disinterested and terminate the encounter.

The generalized habits of flickers among woodpeckers accounts in large measure for the small degree of sympatry exhibited by this genus (e.g., compared with specialized arboreal genera like *Picoides*, *Veniliornis*, etc.). It is no accident that the two known cases of sympatry in flickers involve distantly related species with distinctive foraging habits, behavior, and plumage. These cases involve *Colaptes fernandinae* and *C. auratus* in Cuba, and *C. melanochloros* and *C. campestris* in southeastern South America. Given these cases of sympatry with which to judge the efficacy of possible isolating mechanisms in this genus, it is easy to comprehend the hybridization that occurs between much less well-marked forms within *Colaptes auratus*, *C. melanochloros*, *C. campestris*, and *C. rupicola*.

Pair formation in *C. auratus* seems to come about through attraction of the female to a territorial male, repeated largely agonistic encounters between them, and reinforcement by male to male and female to female agonistic encounters with trespassers in the presence of a prospective mate. As in other woodpeckers (Short, 1971b) reactions to another bird encroaching upon a territory are sexually oriented; males respond to invading males, females to invading females. The presence of the prospective mate during the encounter heightens its

intensity. The conspicuousness and intensity of these encounters in *C. auratus* may be partly a result of the brevity of its territorial proclamation—pair formation period, at least in the strongly migratory populations, in which these activities may be compressed into a period of only two weeks.

The sexually dimorphic plumage features of the head are emphasized during displays, particularly the Head Swinging, Head Bobbing, Bill Directing, and Gaping displays. In most flickers the male has a distinct moustache or malar stripe, which, regardless of color, stands out from its surroundings. Females generally have the malar effectively concolored with the throat such that no malar patch shows. In a few species both sexes have distinct malar stripes, but those of the males have red markings lacking in females; these species include *C. campestris*, *C. rupicola*, and parts of several races of *C. auratus* (females with tan malar patches). In general the color of the malar seems not to matter, as various species have black and red malars, and *C. auratus* has both black-moustached and red-moustached races which freely hybridize. Rather the clear pattern of a malar versus the lack of pattern seems important. In *atricollis* and in some races of *punctigula* males show a crown color difference (more red than females) which also would be emphasized in displays.

Other aspects of color pattern may be involved in agonistic displays. The black chest patch of *C. auratus*, and the black or white throat of *campestris* surrounded by gold coloring to the rear could be intimidatory patterns, the lack of which may preclude effective interbreeding with other species. Such patterns may be important in interactions between *auratus* and *fernandinae*, and between *campestris* and *melanochloros*. The latter two species definitely associate (Short, 1969b) in foraging. Their strong color pattern differences (including green versus brown overall color, spotted versus barred underparts, and large red nuchal versus none), vocal differences, other behavioral differences (Wing Spreading displays of *campestris*, e.g.), the great sociality of *campestris* which may associate in closed little groups all year, and the terrestrial habits of *campestris* (e.g., the tendency of groups of these flickers to fly long distances across open country instead of retreating to the nearest trees when danger threatens) all may serve effectively to prevent interbreeding with

melanochloros. Indeed some of the differences of *campestris* from *piti*us and *rupicola* may reflect the interaction of *campestris* with *melanochloros*.

The great bulk of most populations and indeed of most species of flickers exists without contact with related species. Examples are *C. punctigula* (sympatric only with distantly related species of *Piculus*), *C. atricollis*, *C. rupicola*, and *C. piti*us. It is not surprising to find color pattern reduction in certain of these allopatric species. In *rupicola* the malar pattern is reduced, the red of the male's malar tending to occur only posteriorly. In *piti*us the reduction in pattern is extreme; the bird is entirely barred with an obscure grayish crown, and the male's malar is so reduced that sexual differences are not apparent at a distance.

The nuchal patch may play a role either in intimidation or appeasement. Since this pattern is variable even intraspecifically, great weight cannot be placed on it as a potential isolating mechanism. The red nuchal patch is extensive in all three of the green flickers, it is moderate or absent in different races of both *auratus* and *rupicola*, and it is lacking (aberrant birds occasionally have traces) in *fernandinae*, *campestris*, and *piti*us. An extensive red nuchal, perhaps partly erectile may be employed in Head Swinging or other displays. It is noteworthy that both cases of sympatry in flickers involve one species lacking a nuchal (*fernandinae*, *campestris*) and the other with a moderate (*C. auratus chrysocaulosus*) or extensive (*melanochloros*) nuchal patch.

I found in *Picoides* (Short, 1971b) that displays tended to be similar from species to species, whereas vocalizations showed greater differences. The same seems to obtain in flickers. Employment of an inappropriate vocalization in conjunction with a flawless visual display may result in incorrect responses during interspecific interactions. The rather intricate details and nuances possible with a combined Head Swinging-Head Bobbing-Wicka Call display are important in this context. Strong color pattern differences coupled with any inappropriateness of response would operate to effect reproductive isolation between interacting nonconspecific flickers. On the other hand minor differences in pattern, especially replacement of colors without basic changes in the nature of the pattern, and minor differences within vocalizations (as opposed to differences in the particular vocalization employed) seem easily overcome, allow-

TABLE 24
SUMMARY OF FEATURES OF FLICKERS

	<i>atricollis</i>	<i>punctigula</i>	<i>melanochloros</i>	<i>auratus</i>	<i>fernandinae</i>	<i>pitius</i>	<i>rupicola</i>	<i>campestris</i>	<i>Piculus</i>
Whistled Call	—	(+)	—	—	?	+	+	+	—
Wick Call	—	+	—	—	?	?	?	+	?
Colonial nesting	—	—	—	—	—	—	+	+	—
Terrestrial foraging	(+?)	+	+	++	++	++	+++	+++	—
Terrestrial nesting	—	—	—	—	—	(+)	+	(+)	—
Walking gait	—	—	—	—	—	—	+	+	—
Spotted underparts	—	+	+	+	—	—	—	—	—
Barred underparts	+	—	—	—	+	+	(+)	+	+
Nuchal patch	++	++	++	(+)	—	—	(+)	—	++
Rump patch	(+)	—	(+)	+	—	++	++	++	—
Flash color in tail	+	+	(+)	++	+	—	(+)	—	(+)
♀ malar as throat	+	+	+	(+)	+	+	—	—	+
Green above	+	+	+	tr	—	—	—	—	+
Pale eyes	—	—	—	—	—	+	+	—	—
Broad bill	—	—	—	—	—	+	++	++	(+)
Throat streaked or black	+	+	+	—	+	—	—	(+)	+

Symbols: ?, uncertain; +, present; tr, traces; —, absent. Relative degree of development of a character is shown by this increasing gradient: (+), +, ++, +++. Parentheses around a + also may indicate a condition present in some races but not in others. The *Piculus* condition is the summarized or generalized condition found in such species as *P. rivolii*, *P. rubiginosus*, and *P. aeruginosus*.

ing interbreeding of weakly to moderately morphologically divergent populations.

I have observed hundreds of copulations in *Colaptes auratus*; all seem accompanied by little displaying. Once pairs are formed, copulation may ensue at a rate of up to 16 times per day until it slackens off as incubation commences. Usually a flicker forages for a period of time, then takes a favored perch and issues a series of Long Calls. Ultimately the mate responds by flying to the calling bird. Head Swinging and low Wicka Calls may ensue, and the female then solicits and is mounted by the male.

Several similar instances of copulation were observed in Spot-breasted Flickers. In one of these I triggered the action by whistling a "Long Call." Both members of the pair were foraging on the ground in a pasture at the time. The male responded to my call by flying to the top of a small tree, where he then emitted two consecutive Long Calls. The female flew up to join the

male, both Head Swinging as she landed, calling "week-week." Copulation occurred, the female crouching with tail down and to one side, perched crosswise on a branch. After dismounting, the male gave a weak Head Swinging Display marked by the head held very high; he then directed his bill at the female, which flew away. In another case a female uttered a light "phew" call just prior to the copulation.

Repeated copulations were observed between two birds among a group of four Campo Flickers in Corrientes on September 24. Each copulation was preceded by a low Wicka Call (calling bird unknown). The onlooking birds (sex unknown) stepped back each time copulation occurred. The female crouched and fluffed her plumage as in *C. auratus*. The high degree of sociality and group-displaying in this terrestrial species and in *rupicola* may preclude mixed matings with other flickers, even if otherwise possible.

A PHYLOGENY OF FLICKERS

AN ATTEMPT to establish the evolutionary history of flickers, or of any group is fraught with problems when one lacks a fossil record. Nevertheless I believe that it is possible to establish a hypothetical history based on an evaluation of various character states in flickers and in their relatives. The outcome, a scheme of putative relationships, is both realistic in terms of the available data, and highly probable in general if not in all its details.

In order to establish a phylogeny and attempt reconstruction of a history we must determine if possible those derived states of characters, and those states apt to be primitive within the genus. In effect, we must establish the traits apt to be present in the ancestral flicker. Some of the characters utilized are indicated in table 24.

I should dispel any thought that ground-foraging flickers are primitive woodpeckers from which others are derived. All the families of the order Piciformes (including barbets, Capitonidae, the closest relatives of the Picidae) are arboreal. Both the Jynginae and Picumninae, the two subfamilies of the Picidae other than the Picinae (true woodpeckers), are arboreal. Other ground-foraging and terrestrial (*Geocolaptes olivaceus*) woodpeckers seem to have evolved independently from arboreal ancestors other than flickers (Short, 1971a, 1971d). Even the terrestrial flickers show an array of features ranging from zygodactyly to the undulating flight, perching habits, and movements in trees typical of arboreal woodpeckers; these are explainable on the basis of arboreal ancestry, but are difficult to explain if one considers ground woodpeckers as representing primitive (ancestral) picids. Finally, it is unlikely (to say the least) that, with so many arboreal avian groups, one of the most arboreally specialized groups would evolve from terrestrial ancestors.

A basic assumption of this hypothesized history of flickers is that the rate of divergence of sister species from a common ancestor generally is correlated with the time since they began to diverge. It is of course impossible to exclude the possibility of extremely rapid, or extremely slow divergence in any given instance. However, it seems likely that differences in-

volving several or many characters and character complexes generally require more time than few, or, as in the case of *Colaptes campestris campestris* versus *C. c. campestroides*, one (possibly more; e.g., minor behavioral differences may obtain) character.

It is likely that the ancestral flicker was small in size (perhaps the size of *C. punctigula*), nesting arboreally and foraging arboreally for ants. It probably was barred below and green above with a large nuchal patch, a streaked or black throat and, in females, a streaked or black malar, and it probably had red extending forward around a gray or black crown. This species, very like a modern species of *Piculus*, probably shared a common ancestor with *Piculus*. Essentially, then, the primitive character states (table 24) of flickers are believed to be those shared with *Piculus*. Specialized (derived) features are thought to be those (listed in table 24) by which flickers, and especially *Colaptes rupicola* and *C. campestris*, differ from *Piculus*. Initial developments in the flicker line very likely included dorsal barring, and a tendency to forage at the bases of trees. It is possible that a trend toward increased terrestrial foraging was enhanced in derivatives of this species in southern South America and in northern Middle America, the latter to give rise to a terrestrial-foraging Nearctic species which reached Cuba, represented today by *C. fernandinae*, and the former to the southern South American ancestor of the ground flickers. At a somewhat later time a second northern derivative may have invaded northern Middle America and North America, there to replace ancestral *fernandinae* on the continent. Such a northern derivative may have been ancestral to *auratus*. In South America, speciation gave rise to the ancestor of *campestris* and of *pitiuus-rupicola*. These may have evolved in areas that became treeless, forcing, as it were, their strong terrestrial adaptation. The forest-dwelling form in northern South America probably continued to evolve with relatively little change, although at some time a population became isolated in western Peru (ancestral *atricollis*). The ancestor of *pitiuus* and *rupicola* may have invaded the northern Andes along the

forest fringes of the uplands, after which the northern and southern populations became disjunct.

It is hypothesized that the following developments transpired as sequels to those discussed above: the continued terrestrial adaptation of ancestral *campestris* in southern South America and of ancestral *rupicola* in the Andean plateau; invasion of the pampas fringes and subsequent geographic isolation there of ancestral *melanochloros*; and, divergence of ancestral *fernandinae* on Cuba.

On the basis of the degree of morphological and behavioral differences obtaining among the extant derivatives of the forms involved, the following probably took place recently, that is, in the Pleistocene or late Pleistocene:

(1) geographic isolation and divergence of ancestral *cinereicapillus* and ancestral *rupicola-puna* in the Andes

(2) fragmentation and differentiation of elements of ancestral *C. auratus* (see Short, 1965a)

(3) disjunction and differentiation of northeastern (*melanochloros* group) and southwestern (*melanolaimus* group) populations of ancestral *C. melanochloros*

(4) disjunction and evolution of inland and coastal populations of ancestral *C. atricollis*

(5) invasion of Cuba by ancestral *C. auratus*, and subsequent differentiation there of the *chrysocaulosus* group (for history see Short, 1965b)

(6) savanna and forest elements of the *melanochloros* group diverged, respectively, into *C. m. nattereri* and *C. m. melanochloros*

(7) ancestral *C. campestris* evolved into northern black-throated and southern white-throated forms, respectively *C. c. campestris* and *C. c. campestroides*.

Obviously some of these occurred earlier than others; e.g., (6) followed (3). The greater divergence of the forms involved suggests that 1 to 3 preceded 4 to 7, but of course it is impossible to establish precisely their order of occurrence.

There have been general tendencies evident in different lines. These include increased terrestriality probably largely as a consequence of chance extrinsic isolating factors (e.g., isolation in regions with diminishing forests) during the course of speciation in different areas. Larger size is a feature of all the more terrestrially foraging lines, including the *melanolaimus* group

of *C. melanochloros*. Brown dorsal coloration probably evolved independently in *auratus*, *fernandinae*, and the ground flickers, especially as a tendency toward it seems evident in more terrestrial forms of *C. melanochloros* and *C. atricollis*. Reduction of the nuchal patch occurred in all but the forest flicker group. A rump patch tended and still tends to develop in more terrestrially foraging species inhabiting more open country; the rump patch is best developed in the ground flickers. Flash coloring in the tail has been retained or enhanced in all lines except the ground flickers.

The evidence suggests that ground flickers are more specialized (in the sense of having changed more from the ancestral species of *Colaptes*) than other flickers. They have many features developed more fully (e.g., sociality and wing flicking), as well as many features not found in other flickers (e.g., walking gait, ground nesting; see table 24). Their terrestrial foraging and nesting, development of a walking gait (two species), evolution of loud whistled calls and of a Wick Call (at least one species), their colonial nesting and great sociality (two species), different malar patterns of females, loss of bright tail color, pale eyes (two species), and broad bill represent derived character states. So, too, probably is the broadly pronged manubrial spine of the sternum. All of these developments seem directly or indirectly related to their more terrestrial habits in comparison with other flickers. I am uncertain about the significance of the very strong tubercles on the ulnas of species of ground flickers. This appears to be a primitive character state, with reduction of tubercles in green flickers and even more so in *C. auratus*.

Various similarities of *auratus* with the forest flickers (tables 22 to 24, and also weakly pronged manubrial spine, and weak tubercles of the ulna) suggest that it evolved from an ancestor in common with them after the ancestor of *fernandinae* and of the ground flickers had evolved. For example, it is plausible that *fernandinae* and the ground flickers evolved from a barred bellied ancestor, and that ventral spotting common to *auratus* and part of the green flicker group evolved thereafter. Although the behavior of *fernandinae*, and of the green flickers is not very well known, the analysis of data concerning displays, vocalizations, and instrumental sounds shows close similarity of *auratus* with the green flickers.

Admittedly, regarding *auratus* simply as less terrestrially specialized than ground flickers accounts for many of the similarities between *auratus* and the green flickers. However, *fernandinae* is not so terrestrially specialized as the South American ground flickers, yet it is much more divergent from green flickers than is *auratus*. The restriction of *fernandinae* to Cuba, and its greater differences from the green flickers suggest that it evolved earlier than *auratus*, which may have replaced it on the mainland. The ulna of a Lower Pliocene flicker-like woodpecker (Wetmore, 1931) resembles in its strong tubercles the ulna of modern *C. melanochloros*. Flickers more like the green flickers in at least this one trait seem to have been present along with or prior to the ancestor of *C. auratus*; modern *auratus* has weakly developed ulnar tubercles.

The green flickers, least terrestrially adapted among the flickers, and occupying forest areas, the likely habitat of the hypothetical ancestor of *Colaptes*, have not surprisingly diverged least from that ancestor as a group. They exhibit variation in plumage patterns and in behavior that is expected of a primitive group resembling the ancestral flicker stock. The occurrence of Wick Calls, Wing Flicking, and whistled notes suggests that similar species could have given rise to the ground flickers, as well as to other flickers. To some degree their arboreal habits are accounted for by their woodland and forest habitat, but the habits of the *melanolaimus* group in outlying areas such as northern Patagonia suggest that, in the absence of ground flickers and with opportunity for isolation and speciation, green flickers could evolve into highly terrestrial species.

Among the well-differentiated forms considered conspecific but comprising distinctive entities, *Colaptes rupicola puna* and *C. r. cinereicapillus* and the *melanochloros* and *melanolaimus* groups of *C. melanochloros* seem about as distinct (perhaps slightly more so) as the *cafer*, *chrysoides*, and *auratus* groups of *C. auratus* (Short, 1965a). *Colaptes campestris campestris* and *C. c. campetroides* are far more weakly differentiated. The

prevalence of hybridization in flickers perhaps reflects a rather low rate of speciation in this arboreal-terrestrial group, or it may be a result of chance events. The greater speciation of the genus in South America compared with North America is attributable to a greater opportunity for speciation in the former continent, i.e., more effective barriers have occurred in South America than have occurred for birds of such habits in North America.

The existing flickers include only one potential candidate for the status of superspecies, namely the similar, allopatric *punctigula* and *melanochloros*. These species seem much alike morphologically. Behaviorally they appear to show certain strong differences (Wick Call and whistle in *punctigula*, not known in *melanochloros*), but *melanochloros* is insufficiently known to permit full interpretation of these differences. Tentatively I consider them to comprise a superspecies. Within the ground flickers, *pitiis* is probably nearer *rupicola* than it is to *campestris*; but differences in terrestriality, in sociality, in displays, and in vocalizations indicate that it is too distantly related to both to be considered part of a superspecies with either one. Both *rupicola* and *campestris* are highly distinctive morphologically despite their strongly terrestrial habits, and they are not very closely related.

Relationships in a linear list are best shown for the flickers as follows:

Colaptes atricollis
Colaptes [punctigula] punctigula
Colaptes [punctigula] melanochloros
Colaptes auratus
Colaptes fernandinae
Colaptes pitiis
Colaptes rupicola
Colaptes campestris

The genus *Colaptes* should follow *Piculus* in generic and specific lists. The closest extant relatives of *Colaptes* are *Piculus rubiginosus* and especially *Piculus rivolii*. Other relationships of colaptine woodpeckers, including affinities with African groups are discussed by Short (1971c).

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